CALCAREOUS NANNOFOSSILS OF THE BOREAL LOWER CRETACEOUS: APPLICATIONS IN BIOSTRATIGRAPHY & PALAEOCEANOGRAPHY.

David C. Rutledge

Thesis submitted for the degree of Doctor of Philosophy

University College, London

September, 1994

ABSTRACT

The marine Lower Cretaceous sediments of northern, Boreal latitudes yield diverse and well-preserved calcareous nannofossil assemblages. The calcareous nannofloras of nine core and outcrop sections (of Ryazanian-Albian age) in England, Germany, the North Sea, and Barents Sea, are examined in detail (utilising 773 samples). Dense sampling of key outcrop sections (in particular, Speeton) enables calibration of the observed nannofossil events against ammonite zones. The Barents Sea sections, which are shown to be highly condensed, yield the northernmost Lower Cretaceous nannofossils to be described.

The previously chaotic taxonomy of Lower Cretaceous nannofossils is revised, and a major rationalisation of genera proposed - this involves several generic emendations, and twenty five new combinations. Two new genera, *Apertasphaera* and *Neoparhabdolithus*, and nine new species are described - *Apertasphaera jakubowskii*, *Calculites burnettiae*, *Clepsilithus maculosus*, *Cyclagelosphaera papilla*, *Nannoconus inornatus*, *Nannoconus pseudoseptentrionalis*, *Rucinolithus windleyae*, *Tegumentum bergeni* and *Tubodiscus parvus*. In addition, one new subspecies - *Rhagodiscus angustus parvus* - is described, and a number of species are split into informal varieties, to avoid biostratigraphical ambiguity. Following these revisions, the suprageneric classification is reappraised, and a new family - Family Tubodiscaceae - is proposed.

An updated nannofossil zonation scheme for the Ryazanian to Aptian of the Boreal area is presented; this comprises twenty two zones (labelled BC1 to BC22, in ascending order), and a number of additional subzones. Biostratigraphical resolution in the Hauterivian-Barremian is comparable with current ammonite zonations, and enables detailed sequence stratigraphical interpretation. Following the publication of new data from Tethyan sections (Bergen, 1994), the potential for direct inter-regional correlation is investigated; the nannofossil datums utilised generally support traditional, ammonite-based correlations but suggest that, in Boreal areas, the Hauterivian-Barremian boundary should be placed at the top of the *variabilis* ammonite Zone, slightly higher than its current position.

Finally, the palaeoceanographical applications of Lower Cretaceous nannofossils are considered, in the light of new data on modern nannoplankton. Surface water temperature is believed to have been the principal factor controlling species distribution, throughout the history of nannoplankton; the importance of surface water fertility has probably been exaggerated in previous palaeoceanographical studies, which have been hampered by broad taxonomic concepts. There remains much to be done, in deducing the environmental preferences of Cretaceous nannofossils, but the potential for their application to palaeoenvironmental studies is good.

ACKNOWLEDGEMENTS

Thanks to Paul Bown, Jackie Burnett, Thomas Ehrendorfer, Dawn Windley, Steve Starkie, and Brigitta van Niel, who together formed the UCL nannofossil think tank (or drink tank?) of 1990-94. Special thanks to Paul "that's-not-a-nannofossil-it's-a-piece-of-shit" Bown for his good-humoured supervision and, most especially, for his assistance on the SEM; and to not-so-doubting Thomas Ehrendorfer for his encouragement. The taxonomy applied in this thesis owes much to discussion with numerous nannofossil workers, particularly Osman Varol (Varol Research), Jim Bergen (Amoco), Martin Jakubowski and Jason Jeremiah (Shell), Eric de Kaenel and, of course, Paul Bown.

I am indebted to Pete Rawson for his guidance during sampling of the Speeton section, and many subsequent discussions. Thanks also to Bill Dean, for his assistance during sampling of the Atherfield Clay, and company throughout. Thanks to Merton Smelror, of IKU, for arranging sampling of the offshore Norwegian cores, and to Tim Bralower for providing samples from Borehole 81/43 and subsequent correspondence. Thanks to Elisabetta Erba and Davide Castradori for instructing me in quantitative nannopalaeontology and Macintosh computing; thanks also to Francesca Lozar, for taking care of me during my three month stay in Milano.

Very special thanks to Toby Stiles for his beyond-the-call-of-duty photographic service, tolerance as a landlord, and outrageously good company throughout. Thanks also to Jim Davy, for his indispensable technical assistance, and to Alan Lord for maintaining a smooth(ish) running research unit. Thanks to Wads for being Wads, and to everyone else at UCL, particularly Tim Hackwell, Phil "gagging" Dolding, Alex Mitlehner, Spencer Roberts, Llynne McCarthy, Andy Sam, Graham Rose and Harris Kavouras. Thanks for the (albeit slightly beer clouded) memories.

Thanks to Phil Weaver for providing both employment and the chance to diversify my knowledge of (living) nannoplankton, at the Institute of Oceanographic Sciences, and to Rose Edwards for her assistance with the maps, and other services, during those final, IOS stages. Thanks to Brigitta, once again, for her calming, hippy influence during those final, frantic stages. Thanks to Neil Hulme for providing further employment, some big fish, and much debauchery (oh yes, and he can do nannofossils too...).

This research was funded by the Department of Education for Northern Ireland (DENI), to whom I am grateful. Finally, I would like to say a very special *thank you* to my parents for their encouragement and financial support throughout the rather long duration of my postgraduate studies.

CONTENTS

LIST OF FIGURES

CHAPTER 4:

INTRODUCTION

The term **nannoplankton** (*nanno* is Greek for dwarf) is used to describe the smallest and most numerous members of living marine phytoplankton, namely the **coccolithophorid algae**. These unicellular, autotrophic algae secrete minute calcareous scales (**coccoliths**) of diverse morphology, that form a calcareous cell-wall covering (the **coccosphere**). After death of the alga, the coccosphere usually disaggregates and individual coccoliths may be preserved in sea-floor sediments, constituting calcareous nannofossils. The term **calcareous nannofossil** includes a heterogeneous group of organically precipitated calcite bodies, that are united by their diminutive size, of less than 30 microns (<30μm). The vast majority of calcareous nannofossils fall within the 2-15μm size range. Almost all organically formed bodies within this size range are demonstrably composed of calcite; thus "calcareous nannofossil" is hereafter abbreviated to **nannofossil**. The term **nannoflora** is often applied to both living coccolithophorid assemblages and ancient nannofossil assemblages, although the "floral" origin of certain fossil forms is debatable.

The extremely small size of nannofossils necessitates the use of a **Scanning Electron Microscope (SEM)** or high powered **Light Microscope (LM)** for their study. The SEM enables the fine structure of well-preserved nannofossils to be resolved, and is useful in taxonomic studies, but most routine nannofossil work is done on the LM which, despite its lower resolution, enables quick and easy identification of nannofossils in varying states of preservation.

The oldest well substantiated nannofossils are of Late Triassic age. The group underwent considerable diversification during the Jurassic, especially in the latest Jurassic (Tithonian) when nannofossils proliferated to the extent that they became rock-forming in abundance. Thereafter, nannofossils have remained the major constituents of pelagic carbonates, right up to the present day. Despite suffering heavy casualties due to the Cretaceous-Tertiary boundary event, nannoplankton underwent rapid adaptive radiation in the Palaeocene to give diverse Cenozoic assemblages. Living coccolithophores are among the most important primary producers, forming the base of marine food chains, and profoundly influencing ocean chemistry.

Almost all Cretaceous nannofossil species are extinct (most of those which survived the natural evolutionary pressures of the Cretaceous were catastrophically affected by the terminal Cretaceous event), but most are clearly analogous with the coccoliths of modern coccolithophorid algae, and were undoubtedly produced by similar photosynthetic algae. Occasional Cretaceous nannofossils are similar to the structures produced by living calcareous dinoflagellates; others appear similar to modern ascidian (sea squirt) spicules,

suggesting a benthonic (and animal) origin. However, many common Cretaceous nannofossils have no close living analogues - nannoconids, for example, are of unknown biological affinity. Such *incertae sedis* forms are described as **nannoliths**. The distributions of most nannoliths suggest a planktonic origin but, in view of the possible ascidian origin of some forms, the term *nannoplankton* should perhaps be used with more care.

The **Lower Cretaceous** is an especially interesting episode in the history of nannofossils since, in its earlier part, it includes the dramatic proliferation of nannofossils, when they became the major sink for marine carbonate, altering the chemistry of the world's oceans. Many bizarre forms without any living analogues are encountered, and nannoplankton provincialism seems to have been stronger than at any other time in their history. Lower Cretaceous nannofossils of the Boreal Realm (essentially north-west Europe) have been studied quite intensively, due the availability of good nannofossiliferous sections, and their utility in the search for North Sea oil.

Cretaceous nannofossils are extremely diverse and show considerable evolutionary change, providing numerous first and last occurrence datums (= species originations and extinctions) that can be utilised in **biostratigraphy**. These unique evolutionary events are assumed to represent planes of time-equivalence, and used to subdivide the geological column into **zones**. Certain nannofossil species show major temporal fluctuations in abundance, which are often correlatable on a basin-wide scale; these "influx" or "acme" events may be used to define acme zones. Thus, biostratigraphical resolution can be much improved by detailed quantitative investigation. Since the publication of the first workable nannofossil zonations, some 20 years ago, nannofossils have been proven to be extremely useful biostratigraphical tools, and are now routinely utilised by the Ocean Drilling Program (ODP) and petroleum exploration industry. Their ease of preparation and identification, together with their relative lack of susceptibility to environmental control, make nannofossils superior to other microfossils in many biostratigraphical situations. In addition, the extremely small size of nannofossils means that only very small samples are required, and ensures a remarkable resistance to mechanical breakdown - nannofossils are often the only microfossils recovered from turbo-drilled wells (larger microfossils such as foraminifera are destroyed by the drilling process). These attributes make nannofossils ideal for well-site biostratigraphy, in particular. The Tertiary and Quaternary periods have been very finely subdivided using nannofossils; current zonation schemes for the Cretaceous permit rather lower resolution, but this is often still the best attainable in offshore sections. Ammonites provide the basis for the biostratigraphical subdivision of the Lower Cretaceous, with stage boundaries being defined by changes in the ammonite faunas; strong provincialism among ammonites has necessitated the use of different ammonite zonation schemes in disparate areas, with inter-regional correlations

often fairly limited. Current nannofossil zonations for this interval provide rather less resolution than ammonites, but there remains considerable potential for refinement, and for direct inter-regional correlation.

Because of their planktonic origin and associated wide geographical distribution, nannofossils have generally been considered to be less sensitive environmental indicators than other, benthonic microfossil groups. However, many living coccolithophorids have latitudinally defined (temperature controlled) distributions, and warm and cold-water species are easily identified. Fluctuations in the relative abundance of these extant warm/cold water species have been used in Quaternary **palaeoclimatology** studies. The environmental preferences of Cretaceous nannofossils are obviously more difficult to deduce, but many taxa have palaeolatitudinally defined distributions, enabling identification of warm and cold-water species. Living coccolithophorids are also sensitive to the availability of nutrients, and previous work suggests that Cretaceous nannofossils were strongly influenced by nutrient availability. Thus the basin-wide acmes of several species, that are so useful for biostratigraphical correlation, may reflect major climatic or circulatory changes. There remains great potential for the application of nannofossils in **palaeoceanography.**

PROJECT AIMS

The aims of this project may be placed into three principal categories:

1. BIOSTRATIGRAPHICAL

(a) **Refined North Sea zonation scheme** - Test the existing Boreal nannofossil zonations, particularly the schemes of Jakubowski (1987), Crux (1989) and Mutterlose (1991), which contain a number of inconsistencies. There is now a considerable volume of published data on Lower Cretaceous nannofossils of the North Sea area, which could be drawn together more coherently by a single detailed study. Refined taxonomic concepts, new sections, more closely spaced sampling and detailed abundance data should enable improved biostratigraphical resolution. Ammonite-dated outcrop material should enable precise correlation of the resultant zonation with stage boundaries, as they are currently defined in north-west Europe.

(b) **North Sea-Barents Sea correlation** - Examine the geographical applicability of Boreal nannofossil marker species - can the same events be traced synchronously from the southern North Sea to the northern North Sea, and further north into the sub-arctic Barents Sea? Modern nannoplankton are markedly reduced in diversity at polar latitudes, so it should be expected that a proportion of the marker species useful in the North Sea basin will not be found in the Barents Sea, and that any zonation applied to the Barents Sea will necessarily have lower resolution.

(c) **Boreal-Tethyan correlation** - Attempt to correlate high-latitude (Boreal) and low-latitude (Tethyan and North Atlantic) nannofossil zonations. Nannofossils seem to exhibit strong provincialism in the Lower Cretaceous - published Boreal and Tethyan nannofossil zonations appear totally irreconcilable, with workers in each of these provinces utilising entirely different suites of marker species. North Atlantic sections have yielded more diverse nannofloral assemblages than those documented from the Tethyan stratotypes, but this may be due to poor preservation and the concurrent use of broad species concepts in the Tethyan sections. Recent data from the Tethyan stratotypes and North Atlantic (Applegate & Bergen, 1988; Bergen, 1994) suggest that a number of nannofossil species may be useful in correlation between the realms. In any case, nannofossils show less strong provincialism than ammonites during the Lower Cretaceous and are *potentially* more useful for inter-regional correlation. The limits of the Hauterivian and Barremian stages are currently not very confidently defined in northern Europe, due to strongly endemic ammonite faunas; thus if Boreal and Tethyan sections can be accurately correlated using nannofossils there may be a case for redefining stage or substage boundaries in northern Europe.

2. PALAEOCEANOGRAPHICAL

(a) **Nannofossil provincialism** - Assess the true extent of nannofloral provincialism in the Lower Cretaceous, by comparing coeval assemblages from disparate localities, and examine the causes of this provincialism - current hypotheses include surface water temperature, surface water fertility, transgression-regression models, and palaeogeography. It is anticipated that temperature may be the overriding control, as it is with modern nannoplankton. High-latitude, sub-arctic nannofloras of Lower Cretaceous age are virtually undocumented - a study of such assemblages should allow considerable elucidation of the temperature preferences of Cretaceous nannofossils.

(b) **Nannofossil palaeoecology & palaeoclimatic applications** - The Lower Cretaceous is characterised by a number of dramatic sea-level events and macrofaunal turnover events, that must be linked to long-term climatic changes, but the precise nature of these climatic changes is not well documented. A detailed, quantitative examination of nannofloral composition should allow elucidation of the changing palaeoclimatic conditions - the distributions of warm and cold-water species should reflect major climatic trends. Changes in nannofloral composition can be related to various palaeoclimatic proxies, and compared with important events recorded by other fossil groups (especially the well documented influxes of Tethyan or Boreal derived cephalopods). On a smaller scale, it is proposed to test for cyclic variation (Milankovitch scale?) of nannofloras in response to palaeoclimate, by closely spaced sampling of cyclically bedded sediments. Recent works have placed much importance on the high fertility preferences of certain nannofossil taxa, and it is proposed to test the reliability of these "high fertility indices". Certain long-ranging and apparently cosmopolitan species with no clear environmental preferences (e.g.. *Cyclagelosphaera margerelii*) exhibit long-term, basin-wide acmes - if the environmental significance of these events can be discerned then such species could prove to be extremely useful palaeoceanographical tools.

3. TAXONOMIC

The current state of Cretaceous nannofossil taxonomy is somewhat confused, and it is often difficult to reconcile the species concepts of different authors. Too many, clearly synonymous genera are currently used, and a major rationalisation of nannofossil classification is required. Thus it is proposed to analyse selected problematical lineages, with a view to clarifying some of the many ambiguities in nannofossil taxonomy.

STRUCTURE OF THESIS

Taxonomic consistency is an essential, but often overlooked prerequisite to any biostratigraphical or palaeoceanographical study. Previous workers have tended to utilise poorly-defined taxa, providing only the briefest 'Systematic Palaeontology'. Bearing in mind the confused state of Cretaceous nannofossil taxonomy, and the importance of developing a workable, consistent taxonomy, a considerable portion of this thesis is devoted to taxonomic clarification. The Taxonomy chapter forms the foundation of all the biostratigraphical and palaeoceanographical work and is therefore placed before these sections.

CHAPTER 1:

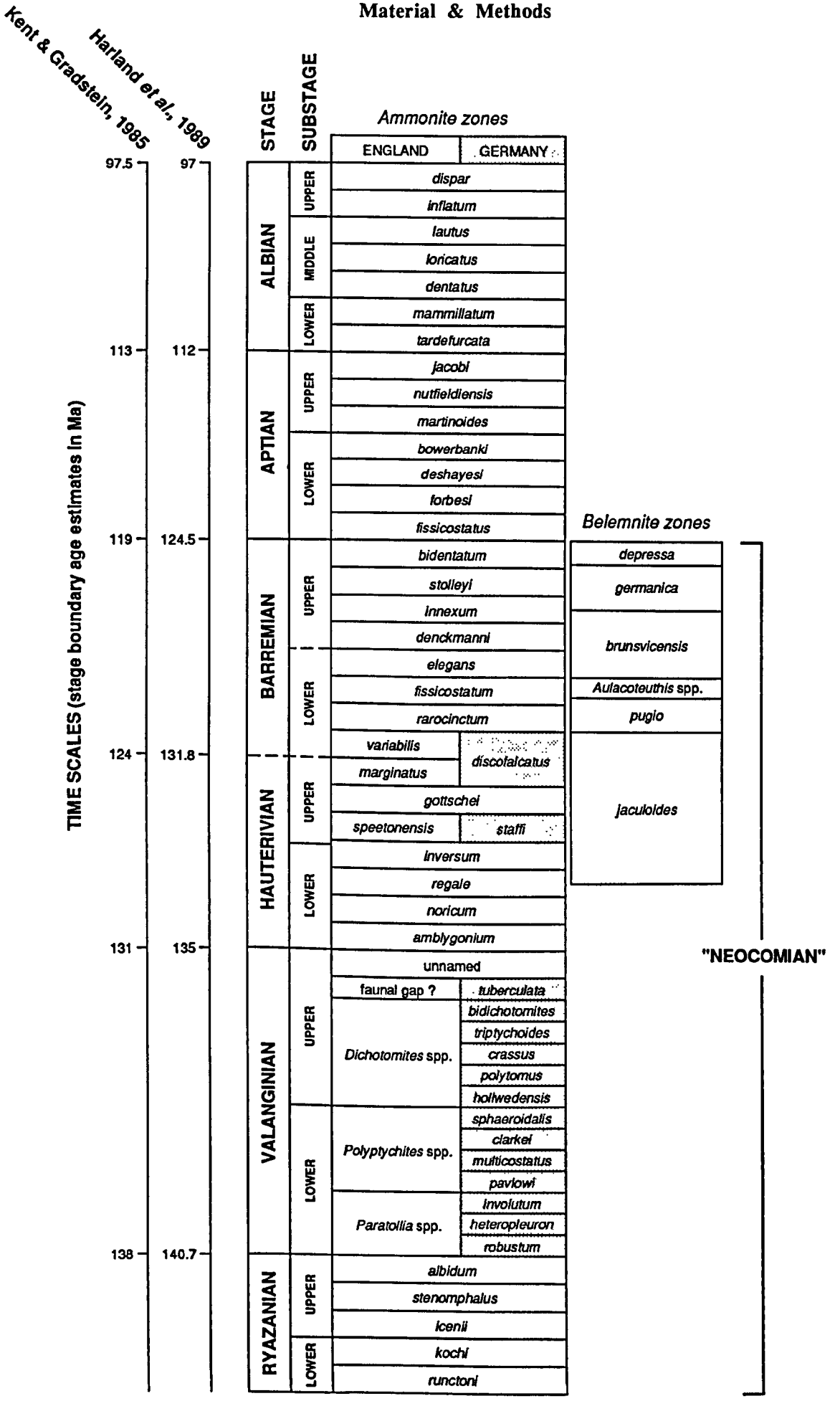
MATERIAL & METHODS

1.1 - CHRONOSTRATIGRAPHICAL FRAMEWORK

Ammonites remain the primary tools for the biostratigraphical subdivision of the Lower Cretaceous, with the six standard stages (Berriasian, Valanginian, Hauterivian, Barremian, Aptian and Albian) defined using the ammonite zonal sequence developed for the type sections of France and Switzerland. However strong provincialism among ammonites has necessitated the development of different ammonite zonations for northern Europe (summarised in Fig. 1.1), which have proven difficult to correlate with the Tethyan standards. Inter-regional correlation is especially difficult within the pre-Aptian part of the Lower Cretaceous - this interval is hereafter referred to as the Neocomian (other authors have used "Neocomian" in more restricted senses, but the term is most usefully applied to the pre-Aptian, when relatively low sea-levels resulted in palaeogeographical isolation, and heightened provincialism among all organisms). Thus a number of stage and substage boundaries are quite tentatively placed in northern Europe. Provincialism is so acute in the uppermost Jurassic and basal Cretaceous that separate stage terminologies are applied: the lowest stage of the Boreal Cretaceous is generally referred to as the Ryazanian and its base (the Volgian-Ryazanian boundary) appears to be younger than the standard (Tithonian-Berriasian) base of the Cretaceous (Rawson *et al.*, 1978).

The zonation outlined in Fig. 1.1 is applicable to England and northern Germany, with much of the Neocomian part of this scheme derived from Speeton, Yorkshire. The Valanginian stage is much better represented in northern Germany, and has been more finely subdivided there. The Hauterivian-Barremian ammonite zonations of England and Germany are closely comparable, but the position of the boundary between these stages remains problematical. Rawson (1971) provisionally placed the Hauterivian-Barremian boundary at the top of his *variabilis* Zone, but following Kemper *et al.* (1981) it is currently placed at the base of this Zone. However in Germany the top of the *discofalcatus* Zone is still generally taken as the Hauterivian-Barremian boundary (e.g.. Mutterlose, 1991); this younger placement approximates Rawson's original (1971) position. Following Kemper *et al.* (1981) the Lower-Upper Hauterivian boundary is placed high in the *inversum* Zone. The position of the Lower-Upper Barremian boundary is much more problematical, but recent finds suggest it might be placed at the top of the *elegans* Zone (P.F. Rawson, manuscript). Ammonites are relatively scarce in the Barremian, which is often more readily zoned using belemnites (Fig. 1.1).

Fig. 1.1 - Chronostratigraphy of the Boreal Lower Cretaceous. Ammonite zones are compiled from Rawson *et al.* (1978), Kemper *et al.* (1981) and Rawson & Mutterlose (1983); belemnite zones are after Rawson & Mutterlose (1983). The tentative placement of the Hauterivian-Barremian boundary is after Kemper *et al.* (1981). Radiometrically based age estimates for the stage boundaries, in million years before present (Ma), tend to vary considerably - thus two alternative time scales (Kent & Gradstein, 1985; Harland *et al.*, 1989) are supplied.


Kent & Gradstein, 1985
Harland et al., 1989
TIME SCALES (stage boundary age estimates in Ma)
97.5
97
113
112
119
124.5
124
131.8
131
135
138
140.7
STAGE
SUBSTAGE
Ammonite zones
ENGLAND
GERMANY
ALBIAN
APTIAN
BARREMIAN
HAUTERIVIAN
VALANGINIAN
RYAZANIAN
UPPER
MIDDLE
LOWER
dispar
inflatum
lautus
loricatus
dentatus
mammillatum
tardefurcata
jacobi
nutfieldiensis
martinoides
bowerbanki
deshayesi
forbesi
fissicostatus
bidentatum
stolleyi
Innexum
denckmanni
elegans
fissicostatum
rarocinctum
variabilis
discofalcatus
marginatus
gottschei
speetonensis
staffi
inversum
regale
noricum
amblygonium
unnamed
faunal gap ?
tuberculata
Dichotomites spp.
bidichotomites
triptychoides
crassus
polytomus
hollwedensis
Polyptychites spp.
sphaeroidalis
clarkei
multicostatus
pavlowi
Paratollia spp.
involutum
heteropleuron
robustum
albidum
stenomphalus
Icenii
kochi
runctoni
Belemnite zones
depressa
germanica
brunsvicensis
Aulacoteuthis spp.
pugio
jaculoides
"NEOCOMIAN"

1.2 - SAMPLING STRATEGY

- geographical and stratigraphical coverage, overlap and density

It was initially intended that this project should cover the entire Lower Cretaceous (Ryazanian-Albian), but thorough coverage of the entire interval proved impossible. Regional hiatuses and barren intervals mean that a large number of sections are needed to give complete coverage. Nine sections were studied in detail (Figs. 1.2 and 1.3) - three outcrop sections (two in England and a composite German section) and six cores (two from onshore England, one from the southern North Sea, one from offshore Mid-Norway, and two from the Barents Sea). All the outcrop material, and some of the core material is accurately dated by means of ammonites/belemnites. In addition a large amount of microfaunal and palynological data is available on the studied sections.

Palaeogeographically, the studied sections span an approximately north-south transect of greater than 2000km, across more than 20° of palaeolatitude, i.e. they are more widely separated than the English or German basins were from Tethys. The Barents Sea sections are notable for yielding the northernmost Lower Cretaceous nannofloras to be described.

The Late Ryazanian-Early Valanginian and Hauterivian-Barremian intervals are well represented in the studied material (Fig. 1.3), with good overlap of section in these intervals. Such overlap enables reliable sequencing of nannofossil events, and comparison of coeval nannofloras. However, despite the large number of sections examined, three intervals remain unsatisfactorily covered:

(1) The lower to 'middle' Ryazanian - This interval is either barren of nannofossils or missing, due to a regional unconformity between the Speeton Clay Formation and the underlying Kimmeridge Clay Formation, in all studied sections. The Berriasian nannofloras of Tethys are well-documented (e.g.. Bralower *et al.*, 1989) but it seems that there is little hope of improving our knowledge of this particular interval in the Boreal area.

(2) The Upper Valanginian - This interval is entirely missing in all but one of the studied sections, due to a major regional hiatus. A few metres of early Upper Valanginian strata are present in BGS Borehole 81/43; the few samples obtained from these beds proved invaluable. This interval is both well represented and richly nannofossiliferous in northern Germany (Mutterlose, 1991) and in parts of the North Sea (David Jutson, *pers. comm.*). There remains considerable potential for improving biostratigraphical resolution within this interval.

(3) The Aptian - In the sections studied this interval is either extremely thin and condensed, due to regional hiatuses, or, where it is thickly developed (as on the Isle of Wight) it is virtually barren of nannofossils.

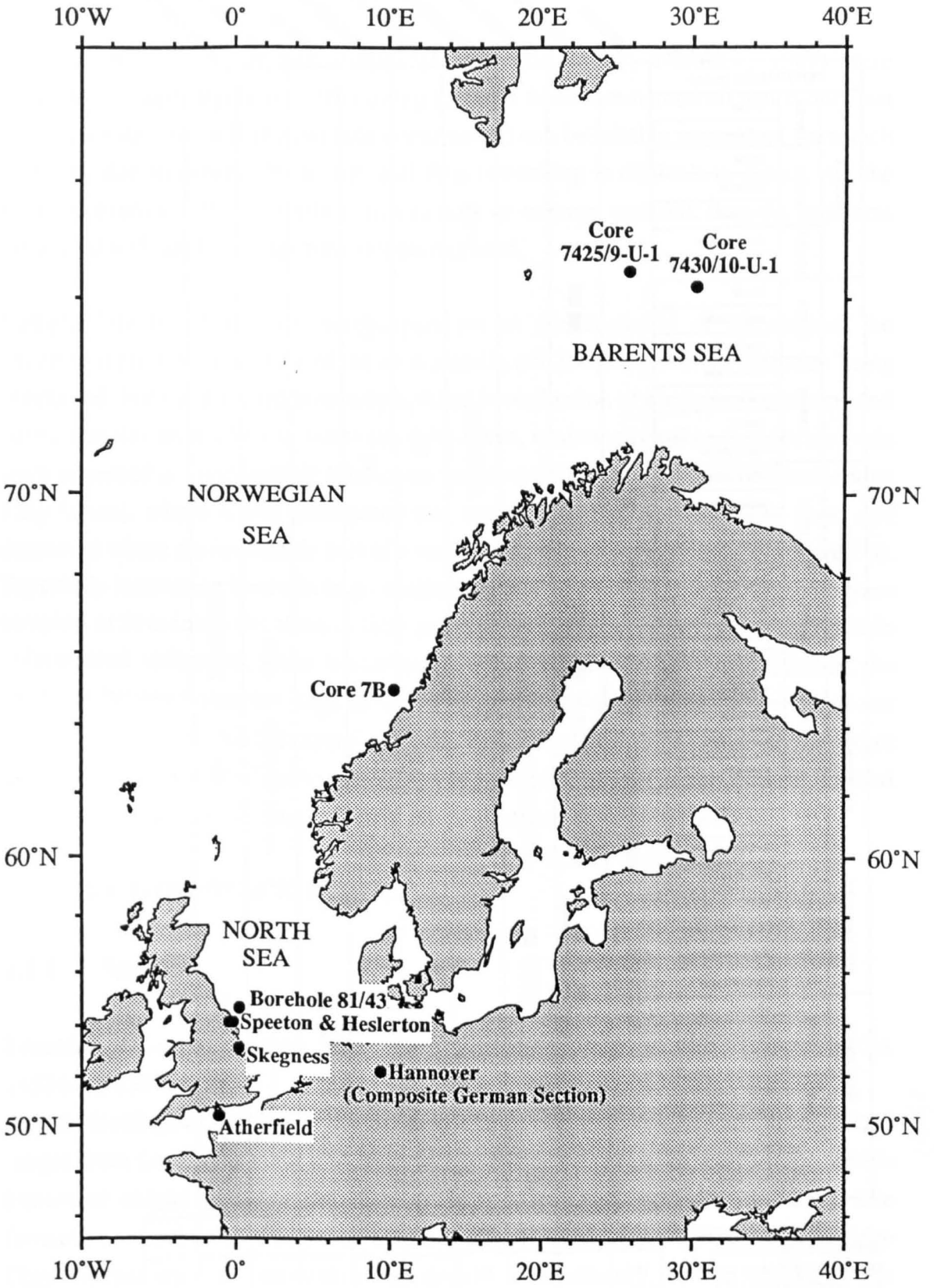


Fig. 1.2 - Locations of the studied sections.

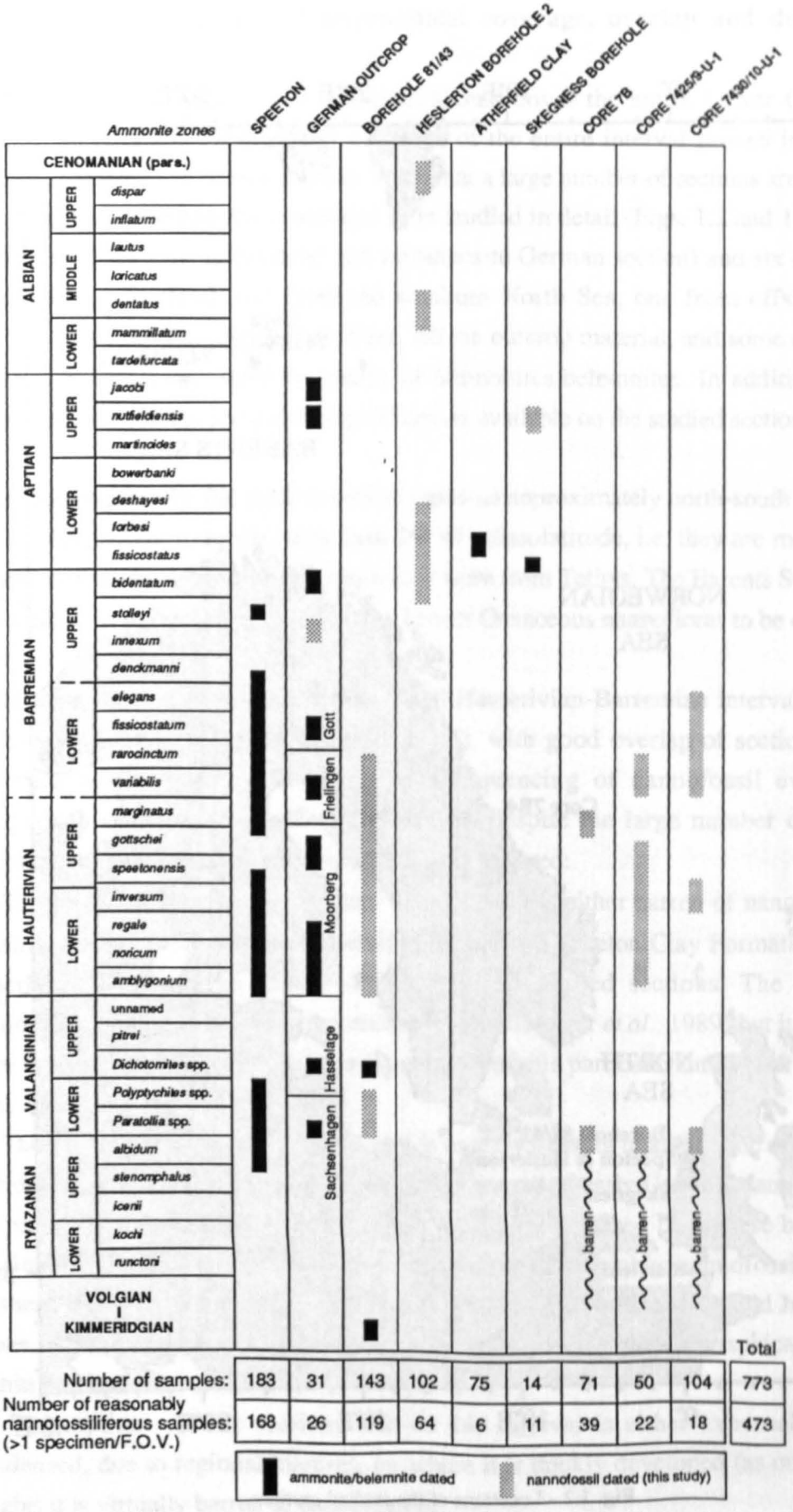


Fig. 1.3 - Stratigraphical extent of the studied sections, and a breakdown of the samples analysed. F.O.V. = field of view (on a light microscope at 1,250x magnification).

Work on the Albian was largely abandoned, despite sampling of the Gault Clay Formation, since this sequence has been the subject of recent detailed biostratigraphical (Jeremiah, *in press*) and palaeoceanographical (Erba *et al.*, 1991) studies.

Several previous North Sea studies (Jakubowski, 1987; Thomsen, 1987) were necessarily based largely on ditch cutting material from commercial oil wells; only last occurrence datums (= first downhole occurrences) can be reliably recognised from such material, due to downhole caving, and thus reworking is difficult to detect. All the material examined in this study is *in situ* core or outcrop material; thus the problems associated with ditch-cuttings were not encountered.

Sample density, or spacing, was dependant on the thickness of the section, the anticipated preservational state of the nannofossils, and the purpose of investigation being conducted. For the standard biostratigraphical investigation of continuous outcrops and cores, samples were taken at intervals of 30-50cm, wherever possible. Sample intervals were increased in unfavourable lithologies (most notably in black shales of Kimmeridge Clay facies), where it was anticipated that nannofossil recovery would be poor, and decreased where the favourable part of a section was thin and condensed (as in Core 7B). Especially interesting intervals (e.g.. cyclic intervals, and faunal change horizons) were sampled at 5cm intervals; there is little point in taking samples any closer than this in unlaminated sediments, since bioturbation will have caused homogenisation of the sediment between samples. Due to the large number of samples examined it was not practicable to plot all the sample depths on lithological logs. Instead, the exact stratigraphical position of each sample (elevation/depth and, for outcrop material, the bed number and ammonite Zone) is given in the range-charts of the Appendix.

1.3 - SECTION DESCRIPTIONS

1.3.1 - Speeton

Location - Coastal outcrop; Filey Bay, Yorkshire, England (Grid Reference TA 145763 to 155754).

Age & Geological Setting - The Speeton Clay Formation (of Rawson *et al.*, 1978) ranges from Late Ryazanian to Albian in age (dated by means of ammonites), and is known to extend offshore into the southern North Sea basin (Rhys, 1974). The formation rests disconformably on strata of Late Kimmeridgian age (the Kimmeridge Clay Formation) and is overlain, apparently conformably, by red chalks of the Hunstanton Formation. Only the Late Ryazanian to Late Barremian interval can generally be sampled from outcrop, due to non-exposure of the upper part of the section. A major stratigraphical break has caused the Upper Valanginian to be missing. Endemic ammonite

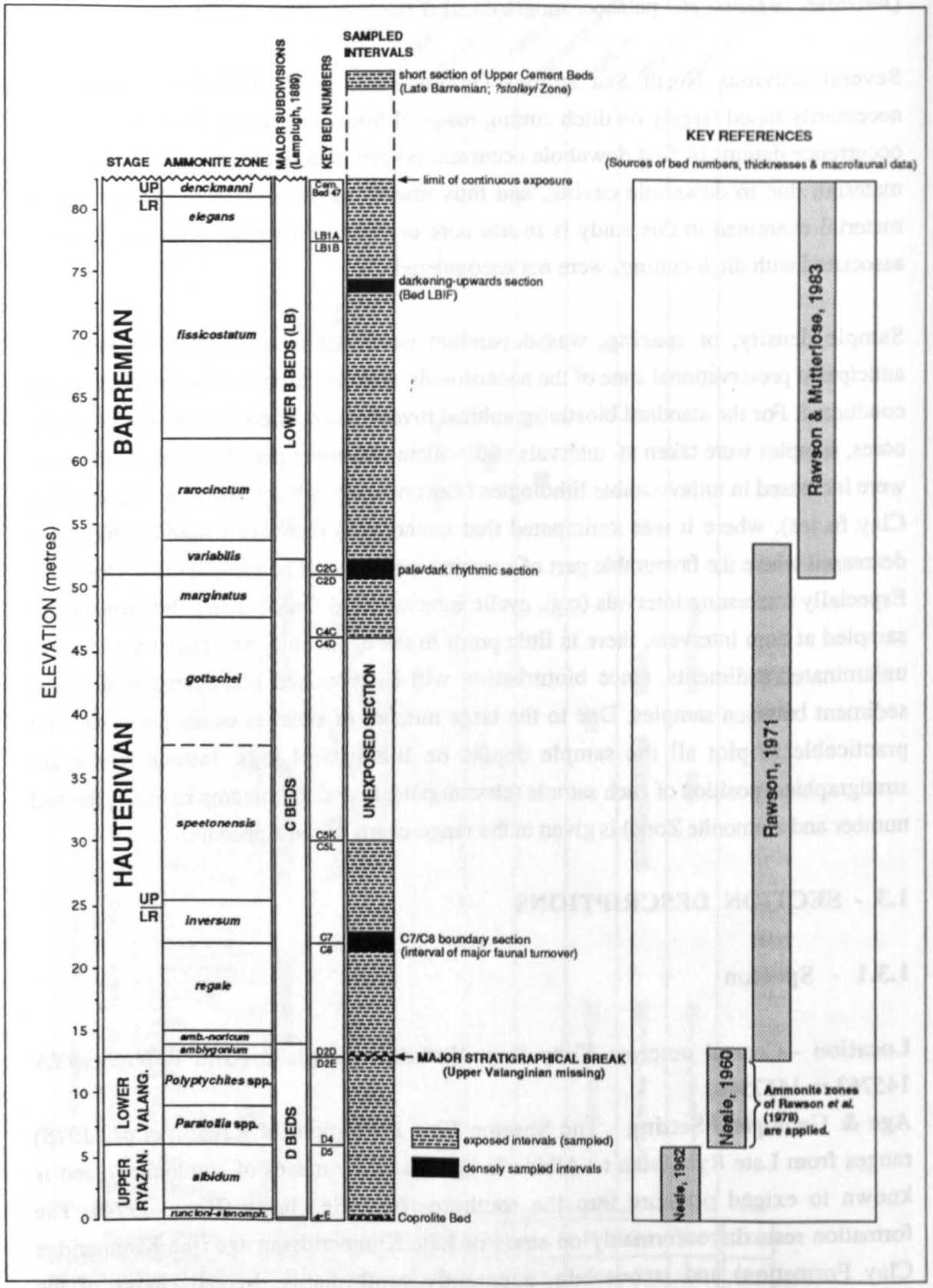


Fig. 1.4 - Summary of the Speeton section, showing sampled intervals and key references for various parts of the section. The bed number and elevation (derived from the above references) of each of the 183 samples is given in the Appendix (Range Chart 1). Elevations are calculated from the base of the Coprolite Bed.

faunas have limited the degree of correlation between Speeton and the Tethyan stratotypes. Several stage and substage boundaries are therefore tentatively placed in this section and, consequently, throughout northern Europe. Inter-regional correlation is especially difficult in the Barremian, but recent finds suggest that the Lower-Upper Barremian boundary should be placed at the top of the *elegans* ammonite Zone (P.F. Rawson, manuscript).

Thickness - The overall thickness of the Speeton Clay Formation is difficult to determine at Speeton (Kaye, 1964), due mainly to slumping, but the sampled section (some 83m) accounts for the bulk of this thickness.

Lithology - Clay/mudstone, generally grey, occasionally silty and/or glauconitic but mainly calcareous, with occasional bands of phosphatic and calcareous nodules.

General References - This richly fossiliferous section is the most complete marine Lower Cretaceous outcrop in Britain, and is generally taken as the type section for the marine Boreal Lower Cretaceous. More than a century of work on the section has allowed detailed lithostratigraphical and biostratigraphical subdivision. Lamplugh (1889) gave the first detailed description, dividing the clays into four major units (A, B, C and D, working downwards) on the basis of their belemnite faunas, with a fifth, basal unit (E, the Coprolite Bed) being defined by its distinctive lithology. Lamplugh further subdivided the D and C Beds on an essentially lithological basis. Subsequent work has resulted in refined lithostratigraphical subdivision of the four major units (Neale, 1960, 1962; Kaye, 1964; Fletcher, 1969; Rawson, 1971; Rawson & Mutterlose, 1983) and the development of detailed ammonite and belemnite stratigraphies (Neale, 1962; Rawson, 1971; Rawson & Mutterlose, 1983). Later workers have followed the slightly unorthodox bed-numbering convention of Lamplugh, with beds being subdivided from the top downwards. Unfortunately there is no single up-to-date work covering the lithostratigraphy and macrofaunal biostratigraphy of the entire section; Fig. 1.4 shows the most useful references for various parts of the section.

Other micropalaeontological work - Neale (1971, 1978) described the ostracod faunas of Speeton, producing an ostracod zonation scheme, while Fletcher (1973) described the foraminifera. Duxbury (1977) proposed a dinoflagellate zonation scheme for the Ryazanian to Barremian of Speeton, and Davey (1979) included data from the section in his formulation of a Late Jurassic to Early Cretaceous dinoflagellate zonation.

Previous nannofossil studies - The excellent preservation of nannofossils within the Speeton Clay made it an attractive subject for early taxonomic studies (Black, 1971; Rood & Barnard, 1972). Subsequent nannofossil studies were mainly biostratigraphical (Sissingh, 1977; Perch-Nielsen, 1979; Taylor, 1978, 1982; Jakubowski, 1987; Crux, 1989). These works show a general trend towards denser sampling and increased taxonomic splitting (as nannofossil taxonomy was refined), with a concomitant increase in biostratigraphical resolution. However, all of these studies have been non-quantitative or, at best (Jakubowski, 1987; Crux, 1989), semi-quantitative, thus limiting their utility

in biostratigraphy and, more particularly, in palaeoceanography. Recent advances in nannofossil taxonomy, and improved documentation of coeval sequences elsewhere (especially in Germany and the North Atlantic) suggested that a thorough re-examination of the Speeton section was required.

Sampling - Slumping of the low cliffs and shifting beach sand make it impossible to sample every bed at any one time. This ever-changing character, and the subtle differences in clay colour by which many of the beds are defined, mean that expert guidance is required. Sampling was conducted under the guidance of Prof. P.F. Rawson, during April of 1991. Every exposed bed was sampled, with several samples being taken from the thicker beds. Detailed sample sets (at 5cm intervals) were taken across cyclic (alternating pale-dark) intervals and horizons of major faunal change (notably across the C7/C8 boundary). 171 samples were collected from outcrop; 12 additional samples from unexposed horizons (previously examined by Crux, 1989, and held by British Petroleum plc.) were subsequently supplied by Dr. Tim Bralower. This density of sampling compares very favourably with previous studies - Taylor (1978, 1982) and Crux (1989) examined 83 and 81 samples, respectively, from equivalent parts of the section. The stratigraphical coverage obtainable from this section is, however, limited by a major break in sedimentation above Bed D2E, which accounts for the absence of Upper Valanginian strata, and by persistent non-exposure of a large part of the Upper Hauterivian (Beds C5K to C4D; a sampling gap of 15.5m). Similarly, although clays of Aptian and Albian age have been proven at Speeton (Kaye, 1964), that part of the section above the *denckmanni* ammonite Zone (Upper Barremian) is rarely exposed. In this respect, I was fortunate in being able to sample a short (c.1.5m) section of the Upper Cement Beds (*?stolleyi* ammonite Zone; Upper Barremian). An additional limitation of the Speeton section is that much of the Upper Ryazanian-Lower Valanginian and the Lower Hauterivian *amblygonium-noricum* Zones are condensed, relative to sections in Germany and elsewhere.

1.3.2 - Heslerton Borehole 2

Location - This shallow, piston-drilled core was taken by the British Geological Survey (BGS), at West Heslerton, about 15km inland from the Speeton outcrop (Fig. 1.6).

Thickness - The entire length of the core was sampled down to its Total Depth of 30m.

Lithology - Approximately 26m of grey-black clays (the upper, unexposed part of the Speeton Clay Formation) are overlain by 2.7m of red chalks and marls (Hunstanton Formation) which, in turn, are overlain by 80cm of white chalk. The transition from clay to red marl/chalk appears to be gradational - there is a gradual increase in carbonate content in the uppermost 50-100cm of the Speeton Clay Formation. The upper part of the clay succession contains five closely-spaced bentonite horizons. The core was logged, at the time of sampling, by Prof. P.F. Rawson and Bill Dean (Fig. 1.5).

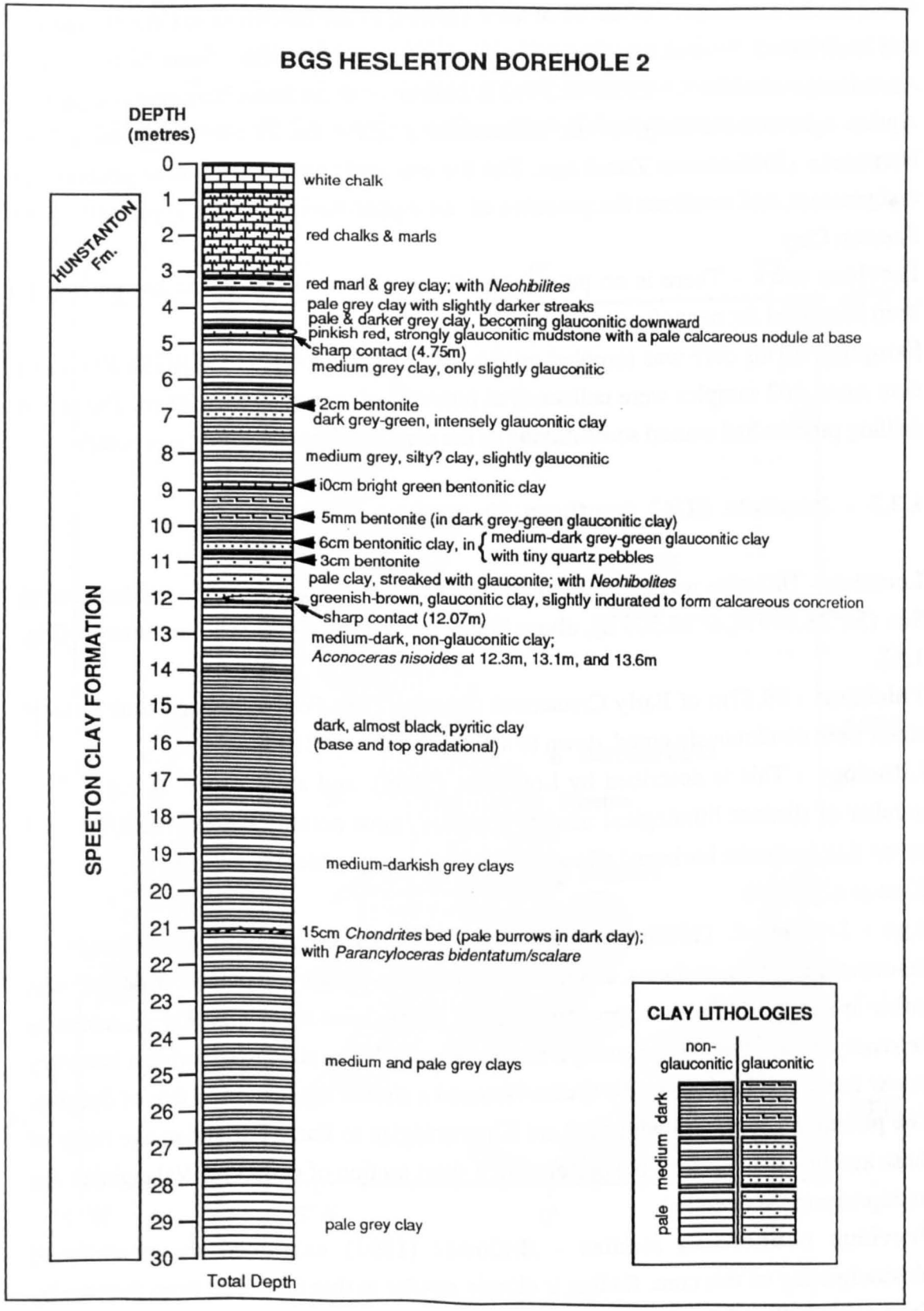


Fig. 1.5 - Lithological log of the Heslerton Borehole, redrawn after Rawson (unpublished). The vertical scale gives depth in metres; sample depths are given in Appendix Chart 9 (102 samples).

Age - Lithologically, this section is very similar to the intermittently exposed uppermost part of the Filey Bay succession, as described by Swinnerton (1935) and Kaye (1964); based on the macrofaunal evidence of these authors, a Late Barremian to Cenomanian age can be inferred. Several age diagnostic ammonites were recorded from the borehole - *Aconoceras nisoides* (at 13.75-12.30m) is indicative of an latest Barremian or earliest Aptian age, and *Parancyloceras bidentatum/scalare* (at 21.10m) suggests a Late Barremian (?*bidentatum* Zone) age. The present study agrees with these general age assignments, and confirms the presence of an Aptian horizon in the upper part of the Speeton Clay.

Previous work - There is no published data on this core, and it had not previously been examined for nannofossils.

Sampling - This core was sampled on the 11th of June, 1991, in the BGS's Keyworth core store. 102 samples were collected; at intervals of approximately 30cm. The piston drilling process had caused some mixing of the clay, so closer sampling was pointless.

1.3.3 - Borehole 81/43 (southern North Sea)

Location - This core was taken by the British Geological Survey, in the southern North Sea (54°38.919'N, 0°14.509'E), about 80km north-east of the Speeton outcrop (Fig. 1.6).

Thickness - 89.87m of Early Cretaceous (Speeton Clay Formation) and Late Jurassic strata were continuously cored, down to a Total Depth of 94.10m.

Lithology - This is described by Lott *et al.* (1986), and summarised in Fig. 1.7. A number of distinct lithological marker horizons (most notably the Coprolite Bed and seven thin bentonite horizons) allow precise lithostratigraphical correlation with Speeton (Lott *et al.*, 1986).

Age - Lott *et al.* (1986) correlated this core with Speeton by means of its lithostratigraphy, macrofauna, and microfauna. However their micofaunal resolution was rather low and they chose to ignore a "middle" Valanginian ammonite (*Karakaschiceras heteroptychum*) at 64.46m, placing a disconformable Valanginian-Hauterivian boundary below this level. Bralower (1991) also assumed a similar succession to that of Speeton. The present study agrees with the Late Kimmeridgian to Early Barremian age range of these authors, but confirms the presence of a short section of early Late Valanginian age (unrepresented at Speeton).

Previous nannofossil studies - Bralower (1991) examined the nannofossil biostratigraphy of this core, finding it closely similar to that described from Speeton by Crux (1989). Based on the ranges of three predominantly Tethyan nannofossil species within this section, he proposed that both the Valanginian-Hauterivian and Hauterivian-Barremian boundaries may have been considerably misplaced at Speeton, and thus throughout northern Europe.

Sampling - Around 180 samples were supplied by Dr. Tim Bralower. Bralower (1991) indicated that below 80m the section was virtually barren of nannofossils, so only a few, marly-looking samples from below this depth were processed. Altogether, 143 samples were processed; 119 of these proved richly nannofossiliferous and were examined in detail. Bralower (1991) chose only 50 "best preserved" samples for his biostratigraphical investigation, but preservation is good throughout most of the samples examined.

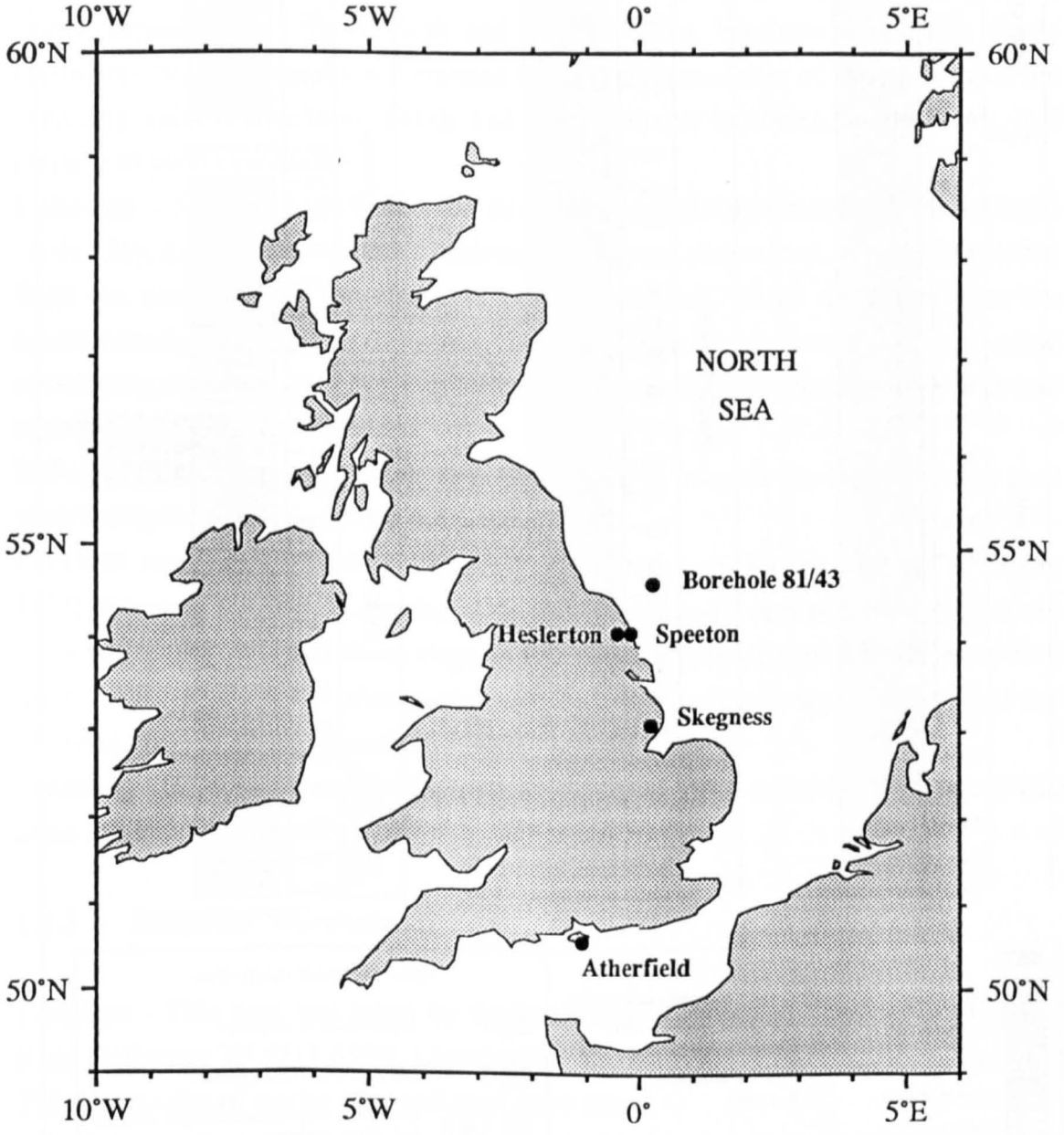


Fig. 1.6 - Locations of the British sections examined in this study.

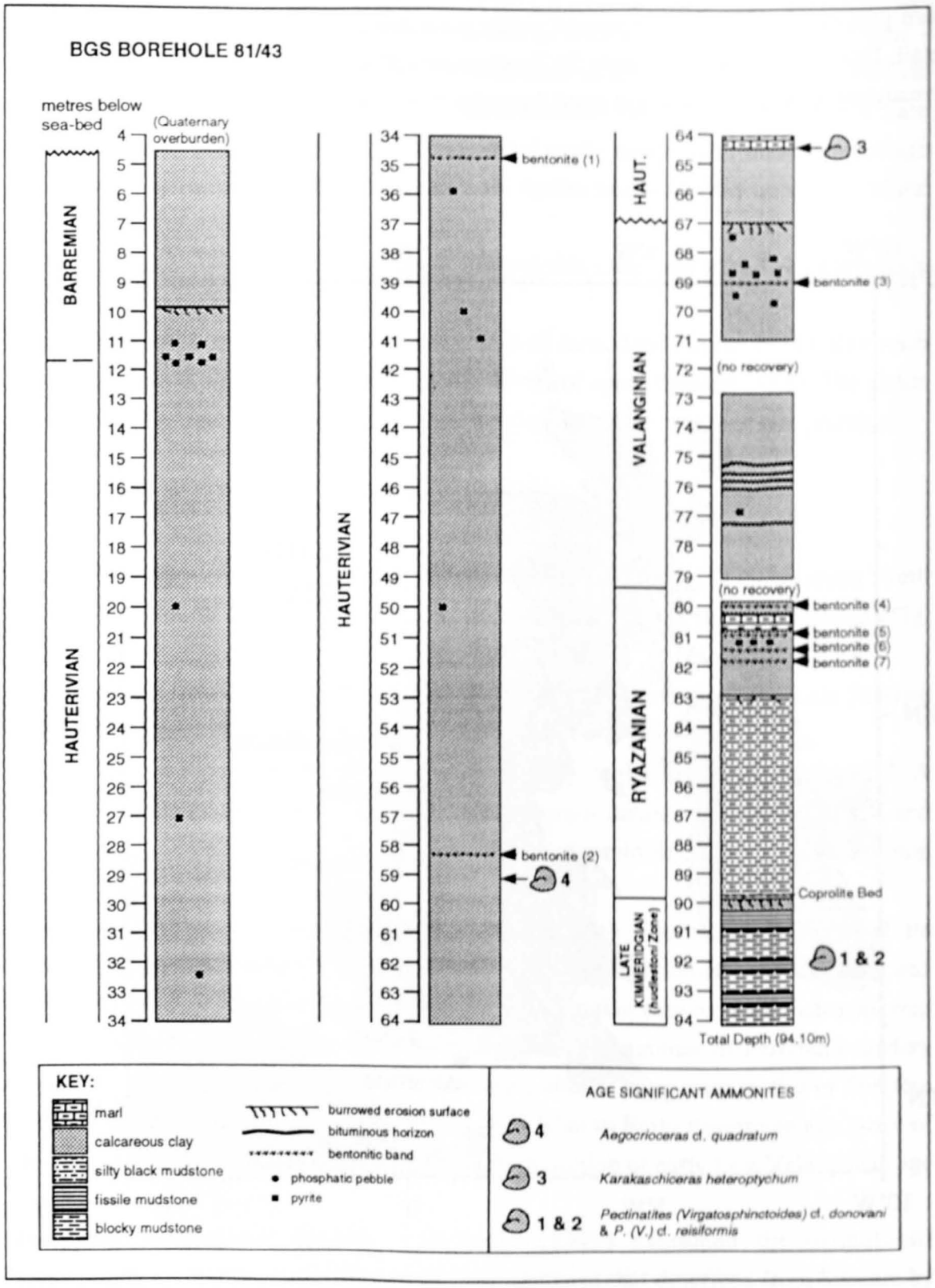


Fig. 1.7 - Summary lithological log of Borehole 81/43, redrawn after Lott *et al.* (1986) and Lott *et al.* (1989). Depth is in metres below sea-bed; sample depths are given in Appendix Chart 3 (143 samples). Stage boundaries are after Lott *et al.* (1989), and are not entirely agreed with in this study (compare with Fig. 3.4).

1.3.4 - Atherfield Clay (Isle of Wight)

Location - Coastal cliff section; Atherfield Point (Grid Reference SZ 45307906), Isle of Wight (Fig. 1.6). This is the type section of the Atherfield Clay Formation.

Thickness - At 55m thick, the Atherfield Clay is the thickest succession of Aptian marine clays exposed in Britain.

Age - Early Aptian; upper *fissicostatus* Zone (*obsoletus* Subzone) to top *forbesi* Zone, applying the ammonite zones of Casey, 1961.

Geological Setting - The Atherfield Clay Formation is a predominantly fine-grained, marine deposit, overlying the fresh and brackish-water, Wealden beds of the Vectis Formation. Marine deposition continued through the remainder of the Aptian, but the overlying units (Ferruginous Sands and Sandrock) are in coarse, sandy facies, and unlikely to yield nannofossils.

Lithology - Simpson (1985) divided this formation into five members: Perna Beds, Chale Clay, Lower Lobster Bed, Crackers, and Upper Lobster Bed, in ascending order. With the exception of the Crackers unit (sandstone), all of these members are predominantly fine grained (clay/silt). The 18m thick succession of pale grey clays constituting the Chale Clay Member looked favourable for nannofossil preservation but, regrettably, this was not the case.

References - Simpson (1985) and Dean (1994) provide up-to-date litho- and biostratigraphical information on this section.

Previous nannofossil studies - Taylor (1981, 1982) and Burnett (*in* Lord & Bown, 1987) examined this section, but found the preservation to be very poor. Jörg Mutterlose (*pers. comm.*) also found these clays to be almost barren of nannofossils. However, nannofossil preservation is often patchy, and it was felt that much denser sampling of this key section might reveal nannofossiliferous horizons.

Sampling - 75 samples were collected during June of 1993, under the guidance of Bill Dean and Martin Simpson.

1.3.5 - Skegness Borehole

Location - This core was taken by the Institute of Geological Sciences at Skegness (Grid Reference TF 5711 6398), Lincolnshire, England (Fig. 1.6).

Thickness - 4m of marine clay and marl were cored.

Lithology - Gallois (1975) describes the detailed lithology of this section, comparing it with the type section of the Sutterby Marl at Sutterby, as it was described from a trench by Swinnerton, 1935. Two metres of marl, closely similar to the Sutterby Marl of Swinnerton (1935), are underlain by a two metre sequence of medium-dark grey clay with *Prodeshayesites bodei*, which Gallois named the Skegness Clay (this was apparently missing from Swinnerton's section).

Age - The ammonite *Prodeshayesites bodei* indicates that the Skegness Clay is of very earliest Aptian age (*bodei* Subzone of the *fissicostatus* Zone); this is significant in that it represents the earliest Aptian marine deposit described in Britain. This interval is possibly represented only as derived material in a nodule bed at the base of the Atherfield Clay (Casey, 1961). The overlying Sutterby Marl is presumed to be Late Aptian in age, although no definitive index fossils were recorded.

Previous nannofossil studies - Black (1971) recorded an excellently preserved nannoflora from the Sutterby Marl of another borehole at Alford, Lincolnshire. Taylor (1982) examined the Skegness Borehole.

Sampling - Taylor's original 14 samples were re-examined; 8 of these are from the Skegness Clay and 6 from the Sutterby Marl.

1.3.6 - Core 7B (offshore Mid-Norway)

Location - This core was taken by the Institutt for kontinentalsokkelundersokelser (IKU), close to the eastern margin of the Trondelag Platform, offshore Helgeland, Mid-Norway (65°06.0'N, 10°17.3'E).

Thickness - 24.05m of Mesozoic strata were cored, down to a Total Depth of 28.55m. Drilling problems resulted in patchy recovery of the uppermost 5m of this section.

Lithology (Fig. 1.8) - The lowermost 17.55m consists of black, organic-rich shale, of typical Kimmeridge Clay facies. This is succeeded by 3m of pale grey limestone/marl. The uppermost, patchily recovered 4m of section consists of red-brown, calcareous mudstone.

Age - An unpublished IKU Report (1982) dates this core as Ryazanian to ?Aptian, with the upper, carbonate-rich portion of the core spanning this entire range. An Aptian age for the core top was based on nannofossil data, although the microfaunal evidence suggested an older (Hauterivian/Barremian) age. Aarhus *et al.*. (1986) reinterpreted the same data (macrofaunal, microfaunal, palynological and nannofossil), to date the core as Ryazanian to Early Barremian, with the bulk of the carbonate-rich part of the core assigned to the Hauterivian. Crux (1989) used nannofossils to date the calcareous part of the core (above 11m) as Late Ryazanian to latest Hauterivian or earliest Barremian, with a stratigraphical break at about 8m accounting for loss of most of the Valanginian and Hauterivian. The present study is in agreement with the findings of Crux, although the uppermost part of the core is dated more precisely, as Late Hauterivian.

Previous nannofossil studies - Verdenius (in Aarhus *et al.*, 1986) and Crux (1989) conducted non-quantitative studies on this section.

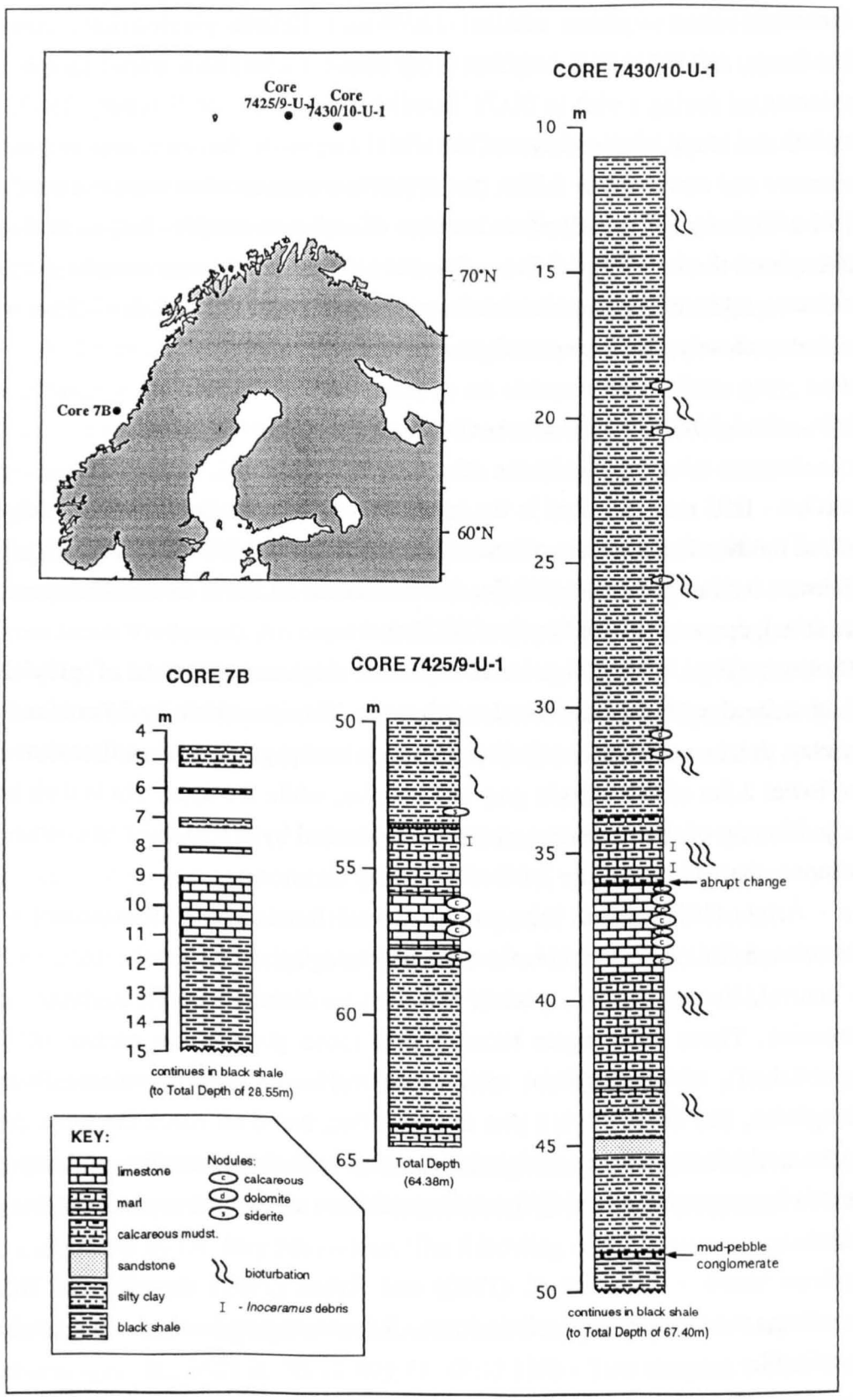


Fig. 1.8 - Summary lithological logs and locations of the three sampled IKU cores. The lithological logs are modified after Aarhus *et al.* (1986) and Århus (1991). Sample depths are given in Appendix Charts 4-6.

Sampling - 31 slides taken from the upper, calcareous part of the Core 7B (4.50-10.95m) were supplied by Martin Jakubowski (Shell); several of these slides were found to be mislabelled - slides labelled 11.70 and 10.00B yielded Late Hauterivian nannofloras, and must thus originate from above 7.35m. This initial sample set was supplemented during a visit to IKU's Trondheim core store (in February, 1993), when I sampled the black shales down to the Total Depth of the core, and resampled the limestones and marls below 9.20m (the uppermost core sections were not available). In all, 71 samples were examined - a number of replicate samples helped to dispel any doubts about the labelling of the ready-made slides. An average sampling interval of 10cm was achieved in the core sections above 11.00m - the shales below were not sampled so closely, due to expected poor nannofossil recovery.

1.3.7 - Core 7425/9-U-1 (Barents Sea)

Location - IKU took this core in the south-western Barents Sea, approximately 380km north of the Nordkapp (northernmost Norway), at 254619.3E 742925.3N (Fig. 1.8).
Thickness - After penetrating 49.9m of overburden, 14.5m of Lower Cretaceous strata were cored, down to a Total Depth of 64.38m.
Lithology (Fig. 1.8) - The basal 80cm of this core consists of greyish-green limestone/marl, with abundant bivalve fragments. This is overlain by 5.7m of red-brown, silty clay, that becomes more calcareous towards its top, grading into a limestone horizon - the lower 2.5m of this is light grey and nodular, while the upper 2m is dark grey and marly. The top of the limestone, at 53.5m, is marked by a 3cm band of coarse-grained sandstone, that is followed by 3.6m of grey, silty claystone.
Age - Århus (1991) dated this core as Boreal Berriasian (= Ryazanian) to Early Barremian, based on buchinid bivalves and palynological data. He rather tentatively dated the central, limestone/marl, part of the core as Valanginian/Hauterivian to Early Barremian. These dates agree broadly with those given in an earlier IKU report (unpublished), which dates the section below 55m as undifferentiated Ryazanian-Valanginian, and the overlying part as Barremian, based on much the same data. The present study dates this core as latest Ryazanian to Early Barremian, with most of the Hauterivian represented in highly condensed form within the central limestone/marl horizon.
Previous work - Århus *et al.* (1990) and Århus (1991) describe the lithology, macrofauna and palynology of this core. It had not previously been examined for nannofossils.
Sampling - This core was sampled at IKU's Trondheim core store, in February, 1993. 50 samples were taken, at intervals of 30-50cm.

1.3.8 - Core 7430/10-U-1 (Barents Sea)

Location - This core was taken by IKU in the south-western Barents Sea, approximately 360km north of the Nordkapp, at 301444.2E 741247.8N (about 140km east of 7425/9-U-1).

Thickness - Approximately 56.40m of Lower Cretaceous and Upper Jurassic strata were cored, down to a Total Depth of 67.60m.

Lithology (Fig. 1.8) - The lowest 24m consists of black shales, of typical Kimmeridge Clay facies, with occasional thin, sandy and conglomeratic layers towards the top. Above 43.9m there is an increase in carbonate content, and the shales grade into grey marls over an interval of 0.8m. Around 39m the marls grade into nodular limestones containing abundant bivalve fragments. At 36m there is an abrupt change from grey, nodular limestone to dark, strongly bioturbated marl with abundant inoceramid debris. Around 34m the marl grades into dark grey, silty clay, with occasional dolomite concretions; this lithology forms the remainder of the core (22.7m).

Age - Århus (1991) dated the section of core above 47m as Boreal Berriasian to Lower Barremian, based on bivalves, foraminifera, and palynology, and on limited nannofossil data (from Jacob Verdenius). An unpublished IKU report dates the lower part of the core (67.60m-47m) as latest Kimmeridgian to Early Berriasian, based on bivalves, palynology and ammonites (most notably *Amoeboceras elegans*, at 67.25m). The present study dates the nannofossil-bearing part of the core (above 43m) as latest Ryazanian to middle Barremian.

Previous work - Århus (1991) described the lithology, macrofauna, microfauna, and palynoflora of the upper part of this core (above 47m), and gave brief notes by Jacob Verdenius on nannofossils recorded from the upper part of the limestone unit.

Sampling - This core was sampled at IKU's Trondheim core store in February, 1993. 104 samples were collected, at intervals of about 50cm.

1.3.9 - German outcrop material (composite section)

A limited amount of ammonite/belemnite-dated Valanginian-Aptian material was collected during a field trip organised by the Fourth International Cretaceous Symposium (October, 1992), and guided by Dr. Jörg Mutterlose. The following sections were sampled during this trip:

Sachsenhagen waste disposal site (about 20km west of Hannover; Map Ref. TK 25 Sachsenhagen, Nr. 3621 R: 35 17 300, H: 58 07 150) - Two samples were collected from the earliest Valanginian (*robustum/heteropleuron* ammonite Zone). This is a mixed non-marine/marine sequence, but the samples were associated with a *Platylenticeras* (ammonite) band. The ammonites and lithology of this former clay pit are described by Kemper (1961) and Mutterlose (1984). Crux (1989) and Mutterlose (1991) studied a

considerable number of samples from this section, finding them virtually barren of nannofossils. One studied samples yielded a dissolution-modified nannoflora.

Frielingen clay pit (about 20km north-west of Hannover; Map Ref. TK 25 Garbsen, Nr. 3523, R: 3534275, H: 5817125) - Two samples were collected from this latest Hauterivian or earliest Barremian (*discofalcatus* ammonite Zone), pale-dark, rhythmically bedded sequence (one from a pale bed and the other from an adjacent dark bed); both proved nannofossiliferous. Mutterlose (1984, 1991a) describes the lithology, macrofauna and rhythms of this section, and its nannoflora (1989b, 1991b).

Gott clay pit (about 30km south of Hannover; Map Ref. TK 25 Sarstedt, Nr. 3725, R: 35 60 400, H: 57 90 650) - This pit exposes the most complete Lower Cretaceous section in north-west Germany (Upper Hauterivian to Upper Barremian, unconformably overlain by Upper Aptian). Mutterlose (1984) gives a detailed account of the lithology and macrofauna of the section; his bed numbers and macrofaunal zones are applied below. The Barremian is zoned and dated by means of belemnites, due to the rarity of ammonites in this part of the section. Mutterlose and Harding (1987), Crux (1989) and Mutterlose (1991a) had previously examined the nannofloras of this section. Sixteen samples (labelled Gott (1) to (16), in ascending order) were collected:

Gott (1) to (6) - Hauptblätterton unit (Bed 100); Early Barremian (*Aulacoteuthis* belemnite Zone) - the base of the unit was not seen but the samples were spaced at 40cm, 90cm, 100cm, 60cm, and 80cm, working upwards from Gott (1).

Gott (7) to (10) - from marls in the upper part of the section (*?germanica* belemnite Zone); these were labelled in ascending order and spaced at intervals of about 50cm.

Gott (11) & (12) - from the youngest Barremian clays exposed (*depressa* belemnite Zone) - Gott (11) was taken 1.05m below the unconformable contact with Late Aptian marls (in the upper part of Bed 197) and Gott (12) 15cm below this surface.

Gott (13) to (15) - from the overlying Late Aptian marls (*nutfieldiensis* ammonite Zone); taken at 10cm, 40cm, and 70cm, respectively, above the base of this unit.

Gott (16) - from the overlying latest Aptian shales (*Jacobi* ammonite Zone).

This rather patchy sample set was supplemented by 10 samples from the Hauterivian of **Moorberg Pit** (about 35km south of Hannover; Map Ref. TK 25 Sarstedt, Nr. 3725, R: 35 59 880, H: 57 89 550), collected by Rosanna Taylor and Jason Crux, and held at UCL. These samples are from the following horizons (applying the bed numbers of Mutterlose, 1984):

MO26 - Bed 35/36; upper *gottschei* ammonite Zone
NG41 - lower Bed 41; lower *gottschei* ammonite Zone
NG40 - basal Bed 58; topmost *staffi* ammonite Zone
NG39 - uppermost Bed 66; *staffi* ammonite Zone

MO25 - Bed 67; *staffi* ammonite Zone
MO19 - Bed 81/82; upper *regale* ammonite Zone
MO16 - Bed 92; lower *regale* ammonite Zone
MO13 - lower Bed 96; *noricum/regale* ammonite Zone
MO5 - mid-upper Bed 101; *amblygonium* ammonite Zone
MO2 - lower Bed 101; *amblygonium* ammonite Zone

In addition, one sample (NG 99) was obtained from the Upper Valanginian (*Dichotomites crassus* ammonite Zone) of **Hasselage Sud** (Map Ref. TK 50 Rahden L3516, R: 34 70 75, H: 58 08 15). This section was sampled by Taylor (1978), who recorded only a sparse, dissolution-modified nannoflora.

Thus a composite section of 31 samples spanning most of the Valanginian to Aptian interval was achieved. Jörg Mutterlose has published extensively on the nannofloras of these sections, but some of his species concepts are difficult to reconcile. Thus, the relatively few German samples obtained proved most useful for comparative purposes. The Moorberg material includes a number of samples attributable to the Late Hauterivian *septentrionalis* nannofossil Zone of Crux (1989), an interval that is unexposed at Speeton, and represents the only ammonite-dated material obtained from this interval.

1.3.10 - Other material

Additional Lower Cretaceous material was given only cursory examination (i.e. not counted or logged), due to the time limitations of the project. This material includes:
Gault Clay Formation - These Mid-Late Albian clays are well known for their excellently preserved nannofloras, which formed the basis of the monumental taxonomic work of Black (1972-73). This formation has recently been the subject of very detailed palaeoceanographical (Erba *et al.*, 1991) and biostratigraphical (Jeremiah, *in press*) studies, so it was felt that time would be more profitably spent on older, less well documented sequences. A fairly comprehensive set of samples, collected from the type section at Folkestone (S. England), proved useful during examination of the less well-preserved Albian assemblages from the upper part of the Heslerton Borehole.
Fullers Earth - A few samples were collected from these Late Aptian bentonitic clays. These largely volcanogenic clays had not previously been examined for nannofossils; one sample yielded a reasonable, though dissolution modified, nannoflora.
Tethyan material - A few "spot" samples from France, Poland, Spain and Tunisia were examined. Assemblages were generally quite poorly preserved, with abundant *Nannoconus*.

1.4 - LIGHT MICROSCOPE vs. SCANNING ELECTRON MICROSCOPE

A high powered LM is the standard tool of the nannopalaeontogist; smear slides are quickly and easily prepared and, with experience, identification of nannofossils is similarly quick and easy. Most routine work was done on an Olympus BH-2, using oil emersion lenses with a combined magnification of 1,250x; light micrographs were taken on a Zeiss Photomicroscope Mark II (also at a magnification of 1,250x). All counting was done under cross-polarised illumination. Phase contrast illumination was used to confirm the identification of weakly birefringent species but, with experience, nearly all species can be identified in cross-polarised light (SEM work confirmed that few, if any, weakly birefringent forms had been overlooked). It is important that the stage of a nannopalaeontologist's microscope can be rotated, since the birefringence pattern of a particular nannofossil depends on its orientation relative to the polarising directions.

Scanning Electron Microscopy was carried out on a Jeol J.S.M.-T200 and Zeiss DSM 940 (mainly on the latter). The SEM enables the fine structure of well-preserved nannofossils to be resolved, and is invaluable in taxonomic studies. However diagenetic overgrowth and adhering clay can often obscure most of the detail that might otherwise be visible on the SEM; these coatings are not so much of a problem on the LM, since they are transparent to transmitted light. In any case, many species are more easily identified on the LM, due to their distinctive birefringence patterns. Thomsen (1987) is, to my knowledge, the only nannopalaeontologist to have used the SEM exclusively in a biostratigraphical study, and it is interesting to compare his results with those of LM workers. In this study, the SEM was hardly used prior to completion of all LM work, and was only then used for accurate characterisation of the "mystery bugs" recorded on the LM.

1.5 - SAMPLE PREPARATION

1.5.1 - Smear slide preparation

This was kept as simple as possible. The most important consideration is to avoid contamination, so all implements used should be disposed of or thoroughly cleaned (preferably in dilute hydrochloric acid) between the preparation of each sample. All samples were from core or outcrop, so no selection or cleaning of cutting fragments was required.

Technique - Having exposed a fresh surface on the sample a small amount of sediment is scraped from this surface with a scalpel, directly on to a clean glass slide. After adding a few drops of distilled water, the sediment is mixed into a slurry and smeared thinly and

unevenly across the slide with a wooden toothpick or cocktail stick. The slide is then dried on a hotplate (at about 70°C) and a cover-slip is fixed with Norland optical adhesive, which hardens after 20 minutes under an ultraviolet lamp. The scalpel is scrubbed and rinsed in dilute hydrochloric acid between the preparation of each sample, and the toothpick discarded.

An uneven spread of material across the slide allows areas of different thickness to be surveyed - the thinner areas are suitable for counting and locating small or delicate species, while the thick areas are scanned for larger, rare marker species. Uneven slides may result in slight biasing of counts towards smaller species (Ehrendorfer & Aubry, 1992), but this is probably offset by the tendency of the operator to look for, and record, relatively uncommon marker species (which are generally large) during counting. Many other, more complicated preparation techniques have been described - these involve such extra steps as crushing with a mortar and pestel, treatment with calgon, suspension in water, centrifuging, settling by evaporation to achieve an even spread, and pipetting. These "refinements" are largely unnecessary, and can greatly increase the risk of contamination through the use of non-disposable glass or earthenware. Centrifuging is definitely undesirable in any quantitative study, since it may result in size fractionation of the nannofossils, and loss of the smallest or largest members of an assemblage. Thus, all slides were made direct from raw sediment. The settling technique, as refined by Beaufort (1991), produces slides of even (and quantifiable) grain density, enabling estimation of absolute abundance figures (number of specimens per gram). However, this technique is time consuming and produces slides that are too thin for biostratigraphy, and possibly contaminated (thorough washing of all the glassware involved is difficult, since the use of acid causes etching of the next preparation - T. Ehrendorfer, *pers.comm.*). Thus, if the Beaufort method is used, a replicate set of standard smear slides must be made.

1.5.2 - SEM stub preparation

This is necessarily rather more complicated than smear slide preparation since, for best results, the nannofossils must be cleaned of adhering clay. This is achieved by ultrasonicating and centrifuging. The SEM is not used for quantitative studies, so slight size fractionating of assemblages due to centrifuging is acceptable.

Technique 1 (standard strew) - Some crushed sample material is placed in a beaker of distilled water, and ultrasonicated for about a minute. Upon removal from the ultrasonic tank, the suspension is allowed to settle for a minute before some of the upper water column is pipetted off into a test tube. This suspension is centrifuged at 1000rpm for 60 seconds; the supernatant (containing clay particles) is discarded and the pellet (=

nannofossils) is resuspended in distilled water. This centrifuging procedure is repeated until the supernatant clears, when most of the clay should have been removed. The pellet is resuspended and diluted, and several drops of this suspension are pipetted on to a 13mm circular glass cover-slip, which is dried in an oven (at about 70°C). The cover-slip is mounted on an aluminium SEM stub using colloidal silver, which dries overnight. Finally, the stub is sputter-coated in gold.

Technique 2 (sediment surface) - A small piece of untreated rock (less than about 4mm high) is mounted directly on the stub, using colloidal silver, and coated in gold. In these preparations, most of the sediment surface was obscured by clay, but small pockets of well-preserved and clay-free nannofossils were found at broken surfaces.

It should be noted that SEM preparations of Speeton material were never particularly successful, and samples that were known, from LM work, to contain abundant and well-preserved nannofossils often yielded only sparse, dissolution modified nannofloras on the SEM, or the nannofossils were entirely obscured by clay. Efforts to clear the samples of clay by centrifuging occasionally resulted in loss of the smallest size fraction of nannofossils. The material from Borehole 81/43 was altogether more suitable for SEM work, being more calcareous and less rich in clay.

A number of techniques enable examination of the same nannofossil specimen under both LM and SEM, but these "same specimen" or "specimen transfer" techniques are very time-consuming if preservation is less than perfect. The LM-SEM transfer technique of Gallagher (1988) was tried with limited success.

1.6 - COUNTING TECHNIQUES

1.6.1 - The development & worth of quantitative studies

Early nannofossil studies tended to be purely qualitative, recording only the presence or absence of particular species. Later works (e.g. most DSDP and ODP studies) tended to be semi-quantitative, recording the abundance of particular species as Abundant, Common, Few or Rare (A, C, F or R), with each of these categories being loosely defined in terms of a number of specimens per number of fields of view. The precise definition of these categories has tended to vary considerably between authors, making comparison difficult. Recent years have seen something of a quantitative revolution, with a profusion of different counting techniques being applied, and much statistical analysis of the results. These quantitative studies have generally been palaeoceanographical, seeking to identify fluctuations in the abundance of key species in response to varying climatic or oceanographic conditions. However, the accurate quantification of nannofossil

abundance is also of biostratigraphical value, since "influx" or "acme" events are often correlatable basin-wide (Jakubowski, 1987; Crux, 1987). Such acmes are often more easily recognisable than the discrete first or last occurrence datums of rare marker species.

1.6.2 - Relative vs. absolute abundance

Relative abundance data is easily gathered by counting a standard number of nannofossils, or a standard number of fields of view, and percentaging the figures. However, such percentage data is inherently difficult to interpret because of the interdependency of the figures (fluctuations in the absolute abundance of a single dominant species may affect the percentages of the other species). Thus techniques enabling estimation of "absolute" abundance have been developed (Backman & Shackleton, 1983; Wei, 1988; Beaufort, 1991). Such techniques enable description of abundance in terms of numbers per unit area of a slide (e.g. as specimens per 10 fields of view, or per mm^2) or, more usually, numbers per unit weight of sediment (specimens per gram). Backman and Shackleton (1983) estimated absolute abundance from standard smear slides, assuming that the grain density was constant over each slide and representative of the sample. Later workers (Wei, 1988; Beaufort, 1991) have used elaborate methods of slide preparation, involving weighing and dilution of a known amount of sediment and evaporative settling on to the cover-slip, in order to allow more accurate and reproducible quantification of absolute abundance.

However, none of these techniques yield truly *absolute* figures, since they fail to account for varying dilution of the nannofossils by detrital material. This may not be a major consideration in Neogene pelagic carbonates (to which such techniques were first applied), but it most certainly is in Cretaceous sequences, which are often strikingly rhythmically bedded, with rapid variation in the carbonate/clay content. Thus the absolute abundance figures may be largely influenced by variations in the supply of terrigenous clastic material (clay), rather than variations in phytoplankton productivity. This problem could be alleviated by measuring the carbonate content of every sample, and calibrating the abundance figures against this - say, for instance, that the carbonate content was 50%, then the *per gram sediment* abundance figures could be doubled to give *per gram carbonate* (= phytoplankton) figures. However, besides being time consuming, this modification would remove any impression (artefact or genuine) of variation in overall phytoplankton productivity. This carbonate-calibration technique is not recommended for chalks, where a large amount of the carbonate (of even the smallest size fraction) is not of phytoplanktonic origin - mid-late Cretaceous (and younger) chalks contain a high proportion of planktonic foraminifera, whose fragments are often encountered, as amorphous lumps of carbonate, in nannofossil smear slides.

Bearing in mind the various complications and uncertainties associated with "absolute" abundance techniques, it was decided to opt for relative abundance estimation. It is recognised that the interpretation of such data can be problematical, but percentage data is believed to be the most reproducible and hence the most easily comparable form of data. The relative abundance data acquired should be directly comparable with data collected by Erba, 1986 (from Italian sections), and Mutterlose, 1991a (from German sections).

1.6.3 - Counting technique applied

Smear slides of raw sediment were examined under a polarising light microscope, at a magnification of 1,250x. For each slide, the first 300+ nannofossils (generally 300-400) encountered, in randomly chosen fields of view of approximately equal particle density, were recorded. A maximum of 100 such fields of view were counted; samples yielding less than 300 nannofossils in 100 fields of view were considered to be too heavily affected by dissolution to warrant further counting. The figure counted was increased to 500+ in the upper part of Core 7B, to allow for the huge dominance of one particular species in part of this section. The number of fields of view counted was recorded - this provides some idea of total nannofossil abundance, and enables rough estimation of "absolute" abundance, in terms of number of specimens per field of view.

1.7 - BIOSTRATIGRAPHICAL LOGGING & PRESENTATION OF RESULTS

The basic, unmodified count data is presented in distribution charts (Appendix); this was converted to percentages (in Excel 4.0) for graphic display, and is supplemented in the charts by further occurrence data. The counting procedure applied, which involves the detailed examination of only a few fields of view, is insufficient for biostratigraphical purposes due to the relative rarity of many "marker" species. Most slides were briefly scanned for marker species immediately after counting. After completion of all counting, all reasonably well-preserved slides (and less well-preserved slides from critical intervals) were re-examined for marker species; where such species were found outside the basic count they are recorded on the distribution charts with a spot (•). This is not ideal, since no impression of the relative abundance of those species recorded outside the count is given (• could mean a single specimen, or up to 1 specimen in 5 fields of view), but it is at least consistent.

The Speeton slides, in particular, were re-examined a number of times, as the probable first or last occurrences of previously unused "markers" were identified in other sections, and replicate slides were made in some instances. Borehole 81/43 was the last section to

be examined, and thus the most systematically checked. Data from this section enabled isolation of several intervals in the Speeton section that were given a final re-check; thus most attention was focused towards the first and last occurrences of several species, and discontinuous ranges through the remainder of their stratigraphical range may be an artefact of the late identification of their marker potential. It is difficult to be entirely objective when logging such a large number of slides, since species concepts develop with time and the attention is generally focused on one or two recognised, and anticipated, marker species. Nevertheless, every effort was made to sequence the nannofossil events as reliably as possible. A number of long-ranging species were observed to have discontinuous (environmentally influenced?) distributions, and efforts were made to document their stratigraphical ranges as fully as possible.

1.8 - PRESERVATION ESTIMATES

Primary dissolution of nannofossils at the sediment-water interface and/or subsequent diagenetic processes (dissolution/overgrowth) tend to result in loss of the more delicate species. Whenever possible, only the best preserved assemblages should be used for palaeoecological interpretation, but provided that the degree of modification can be estimated and is taken into account, even strongly modified thanatocoenoses may be useful. It follows that an accurate estimation of nannofossil preservation is essential to any palaeoceanographical study. In this respect, the descriptive scheme of Roth and Thierstein (1973), with modifications by Roth (1983), is most useful. This scheme relies on the LM identification of etching and overgrowth effects, allowing the categorisation of nannofossil preservation as follows:

E-3 - heavily etched
- much fragmented material, only solution-resistant species left

E-2 - moderately etched
- irregular outlines, delicate structures and species dissolved

E-1 - slightly etched
- serrate outlines, partial dissolution of delicate structures

X - excellent
- coccoliths appear pristine

O-1 - slightly overgrown
- extended coccolith elements, thickened cross-bars, etc.

O-2 - moderately overgrown
- delicate central structures obscured

O-3 - heavily overgrown
- coccoliths so overgrown that identification is difficult

Intermediate degrees of etching/overgrowth were recorded in this study using half numbers (e.g. E-1.5 indicates a degree of etching between E-1 and E-2). Both overgrowth and etching effects are commonly seen in the same sample, but one of these processes can generally be seen to have been dominant.

CHAPTER 2:

TAXONOMY

2.1 - INTRODUCTION

2.1.1 - General

Stradner *et al.* (1968) commented that the taxonomy of Lower Cretaceous nannofossils, and their generic classification in particular was, "in a state of turmoil, which sometimes gives the impression of total confusedness". The current state of Cretaceous nannofossil taxonomy is remarkably little improved. Synonyms abound and concepts differ, and new-comers to nannopalaeontology are faced with a bewildering mess of contradictory data, from even contemporary authors. Biostratigraphical resolution has suffered as a result of taxonomic confusion - current Cretaceous zonations offer much lower resolution than Cenozoic schemes, and this reflects the relative establishment of taxonomic concepts within these intervals. Differences in reported ranges are very often due to different species concepts, rather than to diachroneity, reworking or downhole contamination.

Accurate characterisation of nannofossil species is rather more difficult than for other, larger, microfossils which can be manipulated and examined in three dimensions. In addition, nannofossils are more variable in form than most other microfossil groups, and the degree of structural detail that can be discerned, and used in classification, is dependent upon the method of investigation (LM or SEM). They could thus be subdivided almost infinitely on the SEM, using such structural details as element counts, and early EM workers tended to document such features in meticulous detail, creating endless headaches for later LM workers. Nevertheless, most described Cretaceous species are more readily identified on the LM, in states of varying preservation, and the SEM is generally only required for accurate, unambiguous description. Combined use of both LM and SEM provides the optimum amount of structural information.

2.1.2 - In favour of taxonomic splitting

During routine LM work, a large number of light-microscopically distinct, but indeterminate "sp." were recorded, and ear-marked for later SEM confirmation. Thus all the new species described herein can be readily identified on the LM. Most are illustrated by means of both light micrographs (LMs) and scanning electron micrographs (SEMs); those few that could not be found on the SEM are characterised sufficiently by LMs. Light-microscopically distinct forms which still cannot be reconciled with published species are recorded as numbered "sp." (e.g. *Chiastozygus* sp. 1, 2, 3 and 4) - subsequent LM-SEM specimen transfer may show whether these are new species, or belong to species described from electron micrographs.

In addition, certain "marker" species have been subdivided into **subspecies**, where these forms seem to have differing stratigraphical ranges. The term **variety** is used to describe morphologically distinct variants that appear to have identical ranges and may be ontogenetically related; this term is also applied, informally, to variants that may differ in range, but are not yet accurately characterised. In all these instances "splitting" helps to avoid biostratigraphical ambiguity - the various morphotypes described can always be regrouped later if they are found to be conspecific.

Palaeoceanographical studies have been hampered by excessive "lumping"; until we know the real environmental preferences of each, biologically distinct species, it is dangerous to lump together "similar" or even closely related species. Quaternary studies have shown that very similar species of *Gephyrocapsa* (virtually indistinguishable on the LM) can have radically different ecological preferences. Thus the lumped categories of most Cretaceous palaeoceanographers (e.g.*"Z.erectus"* and *"B.constans"*) should be treated with some caution.

There has, in recent years, been a minor revolution in nannopalaeontology, in that various workers have gained confidence in the identification of nannoliths previously regarded as inorganic crystal growths. Such forms, e.g. spicular nannoliths and the various species of *Assipetra* and *Triquetrorhabdulus*, have been overlooked entirely by many previous workers, but can form an important nannofloral component. Several of these forms have extremely good biostratigraphical potential. It is probably worth recording any regularly-shaped birefringent body; if a particular questionable nannolith is found to have a restricted range in several sections then it is probably of organic origin. Forms recorded in samples barren of calcareous nannofossils can be discounted as being inorganic precipitates. Identification of these rudely crystalline forms is, however, difficult in overgrown material.

2.1.3 - In favour of generic rationalisation

Far too many genera are currently used for Cretaceous nannofossils. Early nannofossil workers (especially those using the TEM exclusively) often based their generic subdivisions on central area structures of dubious importance, resulting in a wide variety of poorly defined genera being available for subsequent misuse. Thus, many later authors have used a variety synonymous genera (e.g. *Staurolithites, Vekshinella* and *Vagalapilla*) for clearly related forms, but dumped a diverse array of unrelated forms into "wastebasket" genera such as *Parhabdolithus*. Such taxonomic inconsistency has been propagated throughout the literature, but should not be tolerated any longer. Thus, many species have been recombined, in an effort to rationalise the generic classification. This has resulted in a marked reduction of the number of genera used. Further, extensive SEM

work may show that subdivision of some of these genera is warranted but, for the moment, the relatively basic classification presented here should provide a coherent taxonomic framework. Every effort has been made to integrate the new species described into existing genera - there are already too many monospecific genera, and we should be wary of electing new genera.

2.2 - MORPHOLOGICAL TERMINOLOGY & PRINCIPLES OF CLASSIFICATION

2.2.1 - Introduction

A plethora of morphological terms have been used in the description of nannofossils, with species often being described as having a particular "-lith" morphology (e.g. cyrtolith, caenolith, etc.). Such excessive restriction of terminology is considered undesirable - in this study only a few, very basic morphological types are considered worthy of separate terminology (these are defined below). Almost all nannofossils are immediately assignable to one or other of these types.

Heterococcolith - coccolith composed of variously sized and arranged, modified calcite crystals (= elements). Such coccoliths fall into two distinct categories: muroliths and placoliths.

> **Murolith** - heterococcolith with a distinct, approximately vertically standing marginal wall.
>
> **Placolith** - heterococcolith with several vertically appressed, concavo-convex shields.

Holococcolith - coccolith composed of uniformly-sized, unmodified calcite microcrystals.

Nannolith - aberrant forms that are not clearly analogous with coccoliths.

The term **rim** is used for the marginal, ring-like part of a coccolith surrounding its **central area**, which may be open, variously bridged by bars, or infilled (partially/completely) by calcite granules. Thus, the term rim is applicable to both muroliths (= wall) and placoliths (= shields); it also includes the inner tube cycle that may line the central area of placoliths, and the proximal plate that is characteristic of certain murolith genera (e.g. *Eiffellithus*). Coccoliths are oriented by reference to their position on the living algal cell - the **proximal** surface of a coccolith faces inwards, and touches

the cell wall, while the **distal** surface faces outwards. Nearly all fossil coccoliths are easily oriented in this way, due to the curvature of the rim (concave surface = proximal; convex surface = distal) and distally extending central processes.

2.2.2 - Murolith Morphology

(see Fig. 2.1)

A murolith **wall** typically consists of two cycles of elements - an inner, proximally located cycle and an outer, distally extended cycle. The wall generally flares distally. The **inner, proximal wall cycle** is often poorly developed, and may not extend beyond the proximal margin of the outer wall; this cycle, which may only be visible in proximal view, has been variously described in the literature as a proximal rim, proximal element cycle, or proximal shield. Bown (1987) used the term proximal shield, but it is thought best to restrict the term "shield" to the concavo-convex rim components of placoliths. The arrangement of the elements forming the inner cycle is often difficult to determine, due to their rudimentary nature, but there is often no discernible imbrication. The **outer, distal wall cycle** (= the distal shield of Bown, 1987a) is the dominant cycle, and is formed from either subvertical (non-imbricating) laths or inclined (imbricating) laths. The direction of imbrication is almost invariably clockwise (= dextral) in Mezozoic muroliths. Bown (1987) distinguished two basic types of murolith based on the imbrication of this outer cycle - the **protolith**, whose outer wall is constructed from non-imbricating elements, and the **loxolith**, whose outer wall is imbricate. Certain groups tend to stick to one or other of these types throughout their evolution, e.g. *Parhabdolithus* (*sensu* Bown, 1987a) characteristically has a protolith wall, while *Rhagodiscus* maintains a loxolith wall. Thus, imbrication of the wall elements, and the relative development of inner and outer cycles are primary characteristics used in the definition of some genera. However, in certain murolith groups (e.g. the Chiastozygaceae), the number and location of the attachment points of central area structures may be more fundamental characteristics (a protolith wall might easily become a loxolith wall, by simple inclination of its wall elements, but radical rearrangement of central area structures would require considerably greater mutation). A major innovation to the basic, bicyclic murolith design was the development of an inner, proximal lining of large, platy elements, constituting a **proximal plate**; this tricyclic rim construction is characteristic of the genera *Eiffellithus* and *Diloma*. However, the majority of muroliths have bicyclic walls. Murolith rims vary considerably in shape - besides showing varying degrees of ellipticity they also form a variety of geometric shapes. However, the outline of a coccolith is not considered to have high taxonomic value.

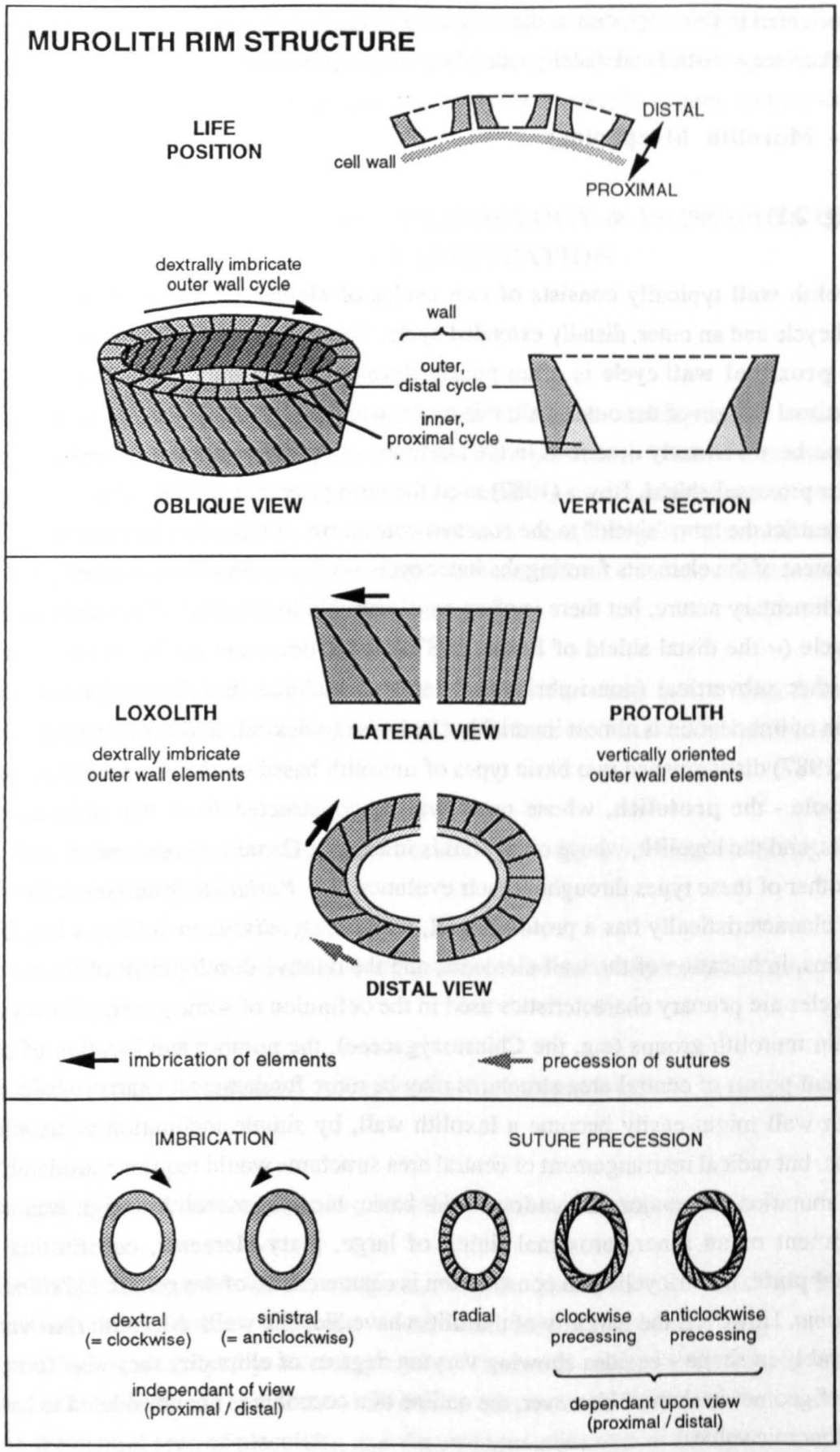


Fig. 2.1 - Morphological terminology applied to the murolith rim.

2.2.3 - Placolith Morphology

The most basic, biscutacean, placolith design comprises two, vertically appressed, concavo-convex **shields**, each consisting of a single cycle of radially arranged, non-imbricate elements; the **proximal and distal shields** are clearly analogous with the inner and outer wall cycles, respectively, of muroliths. However, the saucer-like placolith rim marks a profound change in coccolith construction, enabling interlocking of coccolith margins, and it is proposed that separate "wall" and "shield" terminologies be used for muroliths and placoliths, respectively. The distal shield, which is generally convex outwards, is almost invariably larger than the concave-faced proximal shield.

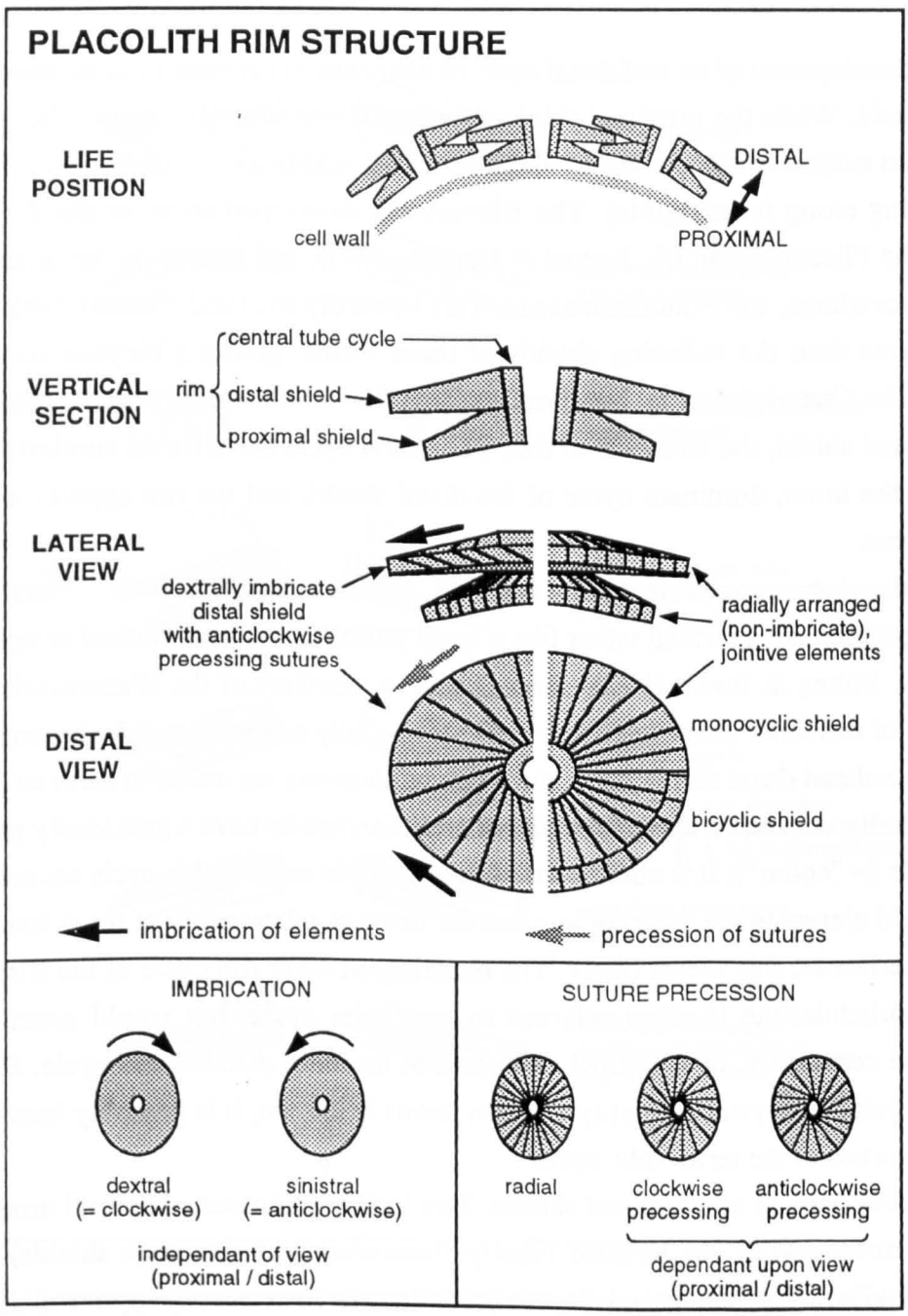


Fig. 2.2 - Morphological terminology applied to the placolith rim.

Bown (1987) recognised two basic types of placolith in the Lower Jurassic - the radiating placolith, with both proximal and distal shields composed of radially arranged, non-imbricate elements, and the imbricating placolith, with a distal shield composed of imbricating elements. These distinctions become slightly blurred in some younger, Cretaceous placoliths (e.g. members of the Cretarhabdaceae), but the most basic, non-imbricate placolith rim is a long-ranging, conservative morphotype (characteristic of the Biscutaceae). This most basic placolith rim consists of two **monocyclic shields**, each composed of a single cycle of elements; besides the development of imbrication, the following major modifications to this basic design are observed in the Mesozoic (see Fig. 2.3):

(1) The development of an additional cycle of elements, at the inner or outer margin of the distal shield. While the proximal shield remained conservatively monocyclic, the distal shield was subject to a good deal of variability, with additional, secondary element cycles developing along its margin(s). The Biscutaceae developed an inner distal rim cycle during the Pliensbachian (de Kaenel & Bergen, 1993), and passed on the innovation to their descendants, the Podorhabdaceae. This inwardly inclined element cycle is more birefringent than the radiating shields of these forms, giving a bicyclic interference pattern. The Cretarhabdaceae, however, developed an additional cycle at the outer margin of the distal shield; the elements of this, peripheral cycle are oriented similarly to those forming the inner, dominant cycle of the distal shield, and the rim appears uniformly birefringent.

(2) The development of a vertically oriented, central **tube cycle** (= the "inner wall" of Bown, 1987a), that is formed rather like a small murolith, from subvertical or imbricating elements. Young & Bown (1991) showed that in members of the Watznaueriaceae the elements of this inner tube cycle are crystallographically continuous with elements of both the proximal and distal shield; these three sets of elements are united to form an "R-Unit" (with radially oriented c-axis). *Tubodiscus* and *Manivitella* have a proximally projecting tube cycle (= "collar"); it is not known whether the elements of this cycle are continuous with shield elements but, bearing in mind the obvious relationship of these forms to the Watznaueriaceae, this seems likely. The birefringent inner rim cycle of the Biscutaceae and Podorhabdaceae is often referred to as a tube cycle, but would seem to have originated separately, by proximal extension of an inner distal shield cycle. However, until the detailed crystal assembly of these forms is known, it is probably best to retain fairly loose use of the term "tube cycle".

(3) The development of additional shields. This innovation occurred several times during the Mesozoic, giving the Jurassic Family Bussoniaceae (with three shields) and the Cretaceous Family Arkhangelskiellaceae (with three or more closely appressed shields).

Young *et al.* (1992) showed that most placoliths are constructed along homologous lines that are rather different to previous models (e.g. Bown, 1987a), with various element cycles that were previously considered entirely separate being crystallographically continuous. There remains much work to be done in deducing phylogenies by means of their new, crystallographically based V/R model. Despite the possible range of variation, certain placolith groups were quite conservative, developing only a few, established rim designs; this enables fairly confident recognition of relationships.

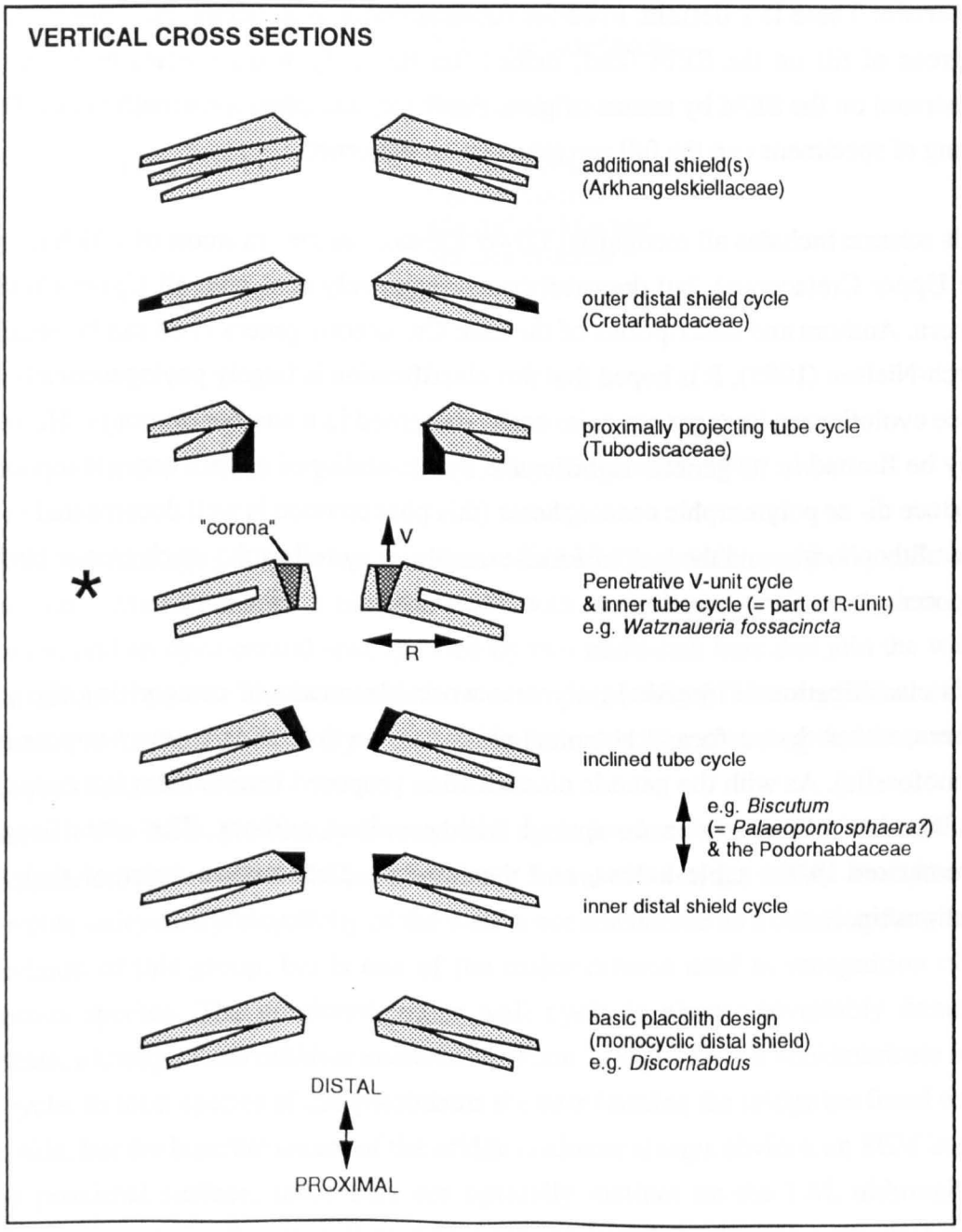


Fig. 2.3 - Some major modifications to the basic placolith design. The cross-sections are rather tentative, in that the detailed crystal assembly of most forms is uncertain; these forms need to be re-examined using the V/R model of Young & Bown, 1991 and Young *et al.*, 1992 (this has been applied to *W.fossacincta* - asterisked).

2.3 - SUPRAGENERIC CLASSIFICATION - A REAPPRAISAL

Numerous authors have attempted suprageneric classifications of Cretaceous nannofossils - Perch-Nielsen (1985) provides the latest and most thorough scheme. Recent taxonomic developments, in particular the rationalisation of genera proposed herein, indicate that these classifications are flawed to some degree. An updated scheme for the suprageneric classification of Cretaceous nannofossils is outlined below. This classification is tentative, since the detailed ultrastructure of many nannofossils remains uncertain. There is a definite need for future authors to illustrate specimens at various degrees of tilt on the SEM (and, indeed, on the LM). Most species have only been illustrated on the SEM by means of plan, distal (or, less often, proximal) views. Only by tilting of specimens can the full rim structure be discerned.

This scheme includes all recognised Lower Cretaceous genera (most of which range into the Upper Cretaceous), but does not comprehensively deal with all Upper Cretaceous genera. Authors and descriptions of the Late Cretaceous genera cited can be obtained in Perch-Nielsen (1985). It is hoped that this classification is largely phylogenetically based, since evolutionary lineages are quite easily discerned in a number of groups. However, it may be limited in its genetic significance by the ability of certain coccolithophorids to produce di- or polymorphic coccospheres (this phenomenon is well documented in living coccolithophorids, and the lack of fossil examples may reflect the much greater likelihood of coccosphere disaggregation).

This classification is intended only as a workable means of categorising the various genera, rather than a formal botanical classification (which is anyway impossible for nannofossils). As with the generic classification proposed herein, there is a reduction in the number of categories compared with previous authors. The classification is summarised in the table below, and the families discussed in order of their likely relationship.

	Family
Muroliths -	Chiastozygaceae Eiffellithaceae Rhagodiscaceae Stephanolithiaceae
Placoliths -	Biscutaceae Podorhabdaceae Cretarhabdaceae Watznaueriaceae Tubodiscaceae Arkhangelskiellaceae
Holococcoliths -	Calyptrosphaeraceae
Nannoliths -	Braarudosphaeraceae Ceratolithaceae Microrhabdulaceae Nannoconaceae Polycyclolithaceae

Family **Chiastozygaceae** Rood, Hay & Barnard, 1973 emend.

Genera - *Chiastozygus*, *Diadorhombus*, *Staurolithites*, *Zeugrhabdotus* (+ *Tranolithus?*).
Definition - Muroliths with a bicyclic wall, with the outer, distally extended cycle dominant, and an open central area spanned by two multi-lath bars that join the wall at four attachment points. The bars may be oriented diagonally (*Chiastozygus*) or axially (*Staurolithites*), or may be closely appressed to form a bridge spanning the short axis of the ellipse (*Zeugrhabdotus*).
Remarks - The inner, proximally-located wall cycle is often vestigial, and the wall may thus appear unicyclic on the LM (and in distal / lateral view on the SEM). Thus, the LM discernible unicyclicity/bicyclicity of the wall is not considered as a criterion for generic subdivision of this group, but is one of the major criteria used in recognition of the numerous species. The dominant, outer wall cycle is almost invariably dextrally imbricate, although *Staurolithites mutterlosei* (Plate 1, Fig. 9) has a non-imbricate outer wall cycle. In most species of *Zeugrhabdotus* the bars forming the bridge are fused on the distal side, but the bipartite nature of the bridge is almost always obvious on SEM images of the proximal surface; these bars are optically distinct on the LM, although the interference pattern is often complicated by a superimposed distal process. *Diadorhombus* has a dextrally imbricate outer wall (Plate 1, Fig. 10), and only differs from *Staurolithites* in having a squarish outline.

CHIASTOZYGACEAE

Fig. 2.4 - Key morphological features and generic differentiation within the Chiastozygaceae.

Family **Eiffellithaceae** Reinhardt, 1965 emend.

Genera - *Diloma*, *Eiffellithus*.

Definition - Muroliths with a bicyclic wall, and a broad, inner, proximal cycle composed of almost horizontally arranged, large platy elements (= the proximal plate), with a central cross arising from the proximal plate. The rim is thus tricyclic.

Remarks - Following Applegate & Bergen (1988), *Eiffellithus* is applied to number of Neocomian forms. *Eiffellithus* and *Diloma* differ in the relative development of their wall cycles (Fig. 2.5). *Eiffellithus* has a vestigial proximal wall cycle (Plate 3, Figs. 5-6; and also observed in *E.turriseiffelii*), which does not extend distally inside the outer wall; thus the rim appears bicyclic on the LM (the broad, inner, proximal plate is brightly birefringent, while the wall is weakly birefringent). *Diloma* has a well-developed, blocky, inner wall cycle that extends to the distal margin of the wall, and forms the bulk of the wall; thus the rim appears tricyclic on the LM. The outer cycle of the wall is imbricate in both genera. *Helicolithus* differs from *Eiffellithus* in having an inner cycle of more blocky elements that are located distally rather than proximally; despite the LM similarities of these genera, *Helicolithus* may have a bicyclic rim, and is possibly more closely-related to *Tranolithus*.

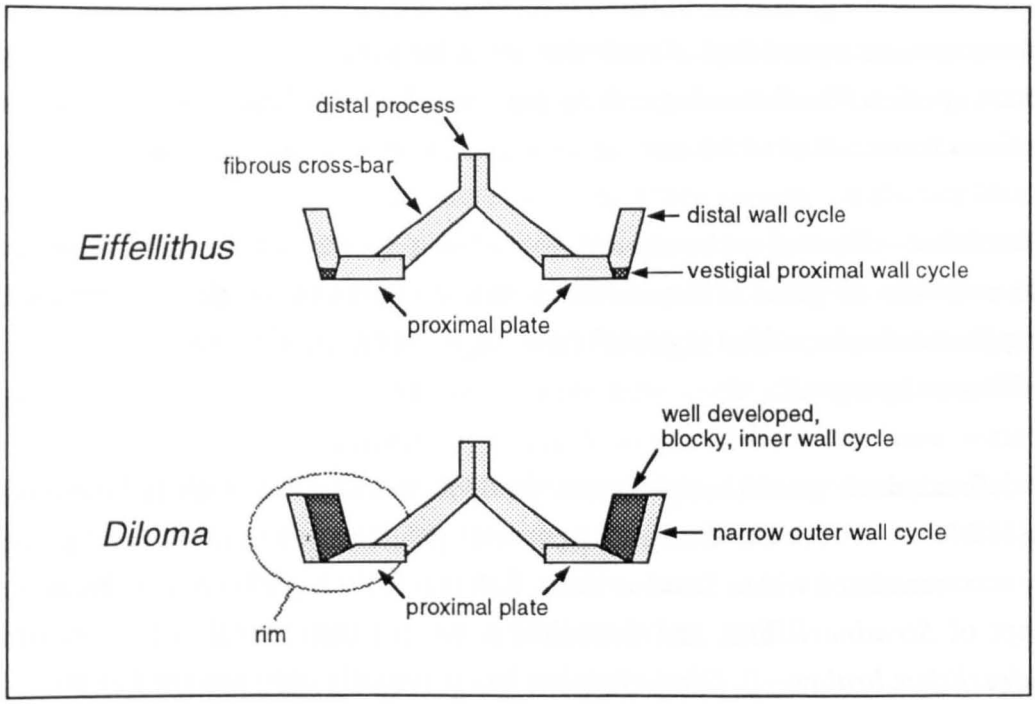


Fig. 2.5 - Tentative vertical cross sections, illustrating the different rim constructions of *Eiffellithus* and *Diloma* (based on *Eiffellithus striatus* and *Diloma galiciense*).

Family **Rhagodiscaceae** Hay, 1977 emend.

Genera - *Calcicalathina, Neoparhabdolithus, Rhagodiscus.*

Definition - Muroliths with a central area filled by granules.

Remarks - Bergen (1994) describes a form intermediate between *Calcicalathina* and *Rhagodiscus*, and these genera are probably closely-related. *Neoparhabdolithus* (gen. nov.) differs from these genera in having a protolith wall (of non-imbricating elements) and a basal grid, but the granular nature of its central area suggests a rhagodiscacean affinity. The walls of *Calcicalathina* and *Rhagodiscus* are essentially unicyclic; the proximal wall cycle is vestigial or absent. The basal grid of *Neoparhabdolithus* probably developed from an inner, proximal wall cycle.

Family **Stephanolithiaceae** Black, 1968

Genera - *Corollithion, Rotelapillus, Stephanolithion, Stradnerlithus, Stoverius?*

Description - Muroliths with a narrow wall of non-imbricate elements, and a wide central area spanned by radially arranged bars.

Remarks - These genera have two wall cycles (as in the Chiastozygaceae) although the inner, proximally located cycle is often vestigial (e.g. in *Stradnerlithus*). The outer, dominant cycle of the wall is composed of approximately vertically arranged, non-

imbricate elements. The central area is spanned by a variable number of radially disposed bars. Various other genera remain poorly defined (see Perch-Nielsen, 1985 for a review), and there remains a good deal of confusion about the generic assignments of a number of common species. The following criteria are applied here to Upper Jurassic and Lower Cretaceous forms, all of which contain some arrangement of radially arranged bars.

Stradnerlithus - elliptical or rhomboidal, with a low, delicate wall (weakly birefringent).
Stephanolithion - elliptical or rhomboidal, with a low wall and laterally projecting spines.
Rotelapillus - circular, with a high wall (birefringent) and lateral spines.
Corollithion - hexagonal.

Thus defined, these genera are phylogenetically distinct. Genera such as *Nodosella* and *Rhombolithion* are considered redundant; species previously assigned to these genera are easily accommodated within *Stradnerlithus*. Rahman & Roth (1991) held a similarly wide concept of *Stradnerlithus*, and described a species transitional with *Rotelapillus* (*Stradnerlithus braloweri*). *Diadorhombus* has previously been assigned to this family (Perch-Nielsen, 1985), but has an imbricate outer wall (Plate 1, Fig. 10; and Applegate & Bergen, 1988, Plate 26) and is probably more akin to *Staurolithites*. The Upper Cretaceous genus *Cylindralithus*, which Perch-Nielsen (1985) assigned to this family, is probably unrelated to the Stephanolithiaceae, and would seem to have placolith affinities. The mid-upper Cretaceous genus *Stoverius* only differs from members of the Chiastozygaceae in having a non-imbricate outer wall; the affinities of this genus remain uncertain, but it gave rise to the hexagonal *Corollithion*. *Scapholithus* is probably related to *Stradnerlithus*, but this extremely long-ranging (Hauterivian to Recent) and conservative genus is sufficiently distinctive to be set aside.

Family **Biscutaceae** Black, 1971 emend. Bown, 1987b

Genera - *Biscutum* (=*Palaeopontosphaera?*), *Crucibiscutum*, *Discorhabdus*, *Similiscutum*, *Seribiscutum*, *Sollasites* (& *Gaarderella?*).
Description - Placoliths with two shields constructed from radially arranged, non-imbricate elements, with or without an inner cycle of inwardly inclined (but non-imbricating) elements. The central area may be imperforate, vacant or spanned by a simple structure (cross or bar).
Remarks - In a recent study of ancestral (Early to Middle Jurassic) biscutaceans, de Kaenel & Bergen (1993) described a new genus, *Similiscutum*, and proposed considerable revision of this family. These authors distinguish *Palaeopontosphaera* (previously widely regarded as a synonym of *Biscutum*) from *Biscutum* by the presence of a birefringent, inner distal rim cycle in the former; if this distinction is followed then a number of Cretaceous species (including the ubiquitous but probably polyspecific

Biscutum constans) should be reassigned to *Palaeopontosphaera*. Pending confirmation of these taxonomic developments, it is probably best to retain the traditional usage of *Biscutum*, but Cretaceous biscutaceans, like their Jurassic predecessors, may have been more diverse than is generally realised. Despite the current confusion surrounding the definition of genera, this remains a relatively conservative and well-defined family. The distinction between an "inner distal shield cycle" and "central tube" is slightly blurred in this family (the former probably gave rise to the latter, by proximal extension) but, whatever the terminology applied, this inner element cycle is easily identified on the LM as a birefringent ring. The central area of *Discorhabdus* is infilled by a birefringent plug (= spine base) that may be analogous with the tube cycle of other genera. The rim structure of *Sollasites* is not discernibly different to that of *Crucibiscutum* (which was misdiagnosed as having imbricate shields by Jakubowski, 1986) and there is little point in setting this genus apart in the Sollasitaceae (as followed by Perch-Nielsen, 1985).

Family **Podorhabdaceae** Noël, 1965

Genera - *Axopodorhabdus*, *Ethmorhabdus*, *Hemipodorhabdus*, *Tetrapodorhabdus*, *?Octocyclus*, *Perissocyclus*.

Description - Placoliths with two narrow shields composed of radially arranged, non-imbricating elements. The inner margin of the rim is lined by a cycle of inwardly sloping, non-imbricating elements. A wide central area is spanned by a mesh-work of granular crystallites; this granular central cover is perforated by a number of windows, generally arranged concentrically around a hollow distal process.

Remarks - This rim construction is light microscopically distinct - the rim appears bicyclic, with a weakly birefringent outer cycle and a birefringent, "beaded" inner cycle. As in the Biscutaceae, the birefringent inner cycle may be part of the distal shield (= inner distal shield cycle) or it may a penetrative, tube-like structure. Perch-Nielsen (1985) placed these forms in Subfamily Podorhabdoideae, of the Family Podorhabdaceae (in which she included cretarhabdaceans), but the "podorhabdid" construction is sufficiently distinctive to warrant family status. De Kaenel & Bergen (1993) demonstrated that the type genus, *Podorhabdus*, is a junior synonym of *Discorhabdus*, but the "podorhabdid" concept is so developed that this family name is best retained. These forms have probably been over-divided in the past (see Perch-Nielsen, 1985) - genera such as *Dekapodorhabdus*, *Dodekapodorhabdus* and *Octopodorhabdus/Octocyclus*, that are defined using the number of central openings, are liable to be either monospecific (*Dekapodorhabdus*, *Dodekapodorhabdus*), or to include forms of disparate age with no direct relationship (*Octopodorhabdus/Octocyclus*). Such genera are probably best abandoned in favour of *Perissocyclus*.

Family Cretarhabdaceae Thierstein, 1973

Genera - *Cretarhabdus, Cruciellipsis, Flabellites, Grantarhabdus, Helenea, Speetonia.*
Description - Placoliths with two shields composed of non- or only slightly imbricating elements, that are predominantly radially arranged. The larger, distal shield is generally bicyclic, with a broad inner cycle of radially arranged elements, and a narrow outer cycle of radially or tangentially arranged (precessing) elements. The monocyclic proximal shield consists of radially arranged elements. The central area is spanned by several fibrous bars, of variable number and arrangement; these often support a distal process, which is always solid.
Remarks - Despite the similarities in rim construction, these forms are readily differentiated from members of the Podorhabdaceae on the LM by the uniform birefringence of their rims (they lack the inner, "beaded" cycle characteristic of podorhabdids). Furthermore, they differ from the Podorhabdaceae in having fibrous (birefringent) central bars, and a solid (rather than hollow) distal process. Numerous other genera of dubious distinction have been proposed for the forms here included in *Cretarhabdus*. Several of the other genera retained are monospecific, but these are very distinctive. *Helenea* (junior synonym = *Microstaurus*) is differentiated by the strong precession of the elements in the outer cycle of its distal shield (on the LM, the rim sutures are visibly offset towards the outer margin). *Helenea* would seem to be the most aberrant member of this family, and may be related to the Watznaueriaceae.

Family Watznaueriaceae Rood, Hay & Barnard, 1971

Genera - *Ansulasphaera, Apertasphaera* (gen. nov.), *Cyclagelosphaera, Watznaueria.*
Description - Placoliths with two broad shields; the wider, distal shield is birefringent. The elements of the main, outer cycle of the distal shield are dextrally imbricate, with anticlockwise precessing sutures. There may be an additional, penetrative and crystallographically separate inner cycle (= the V-unit) and a central tube cycle (that is crystallographically continuous with elements of both shields). The relatively narrow central area may be open, filled by a crystalline plug, or occupied by a variety of structures (bar(s), granular grille, etc.).
Remarks - Young & Bown (1991) showed that in *Watznaueria fossacincta* the elements of the inner tube cycle, proximal shield, and distal shield are crystallographically continuous, constituting an R crystallographic unit. An additional, penetrative tube core cycle (= the V-unit) is crystallographically separate; the distal expression of this cycle is termed the "corona" (to distinguish it from an enclosed inner tube cycle). Where present, the inner tube cycle does not project significantly beyond the rim (*Ansulasphaera* has a tube-like proximal extension, but this is formed from the proximal shield). The presence or absence of this tube cycle is not used as a criterion for generic splitting, due mainly to

the difficulty in applying this distinction on the LM, and *Ellipsagelosphaera* (which might be distinguished by the presence of a tube cycle) is regarded as a junior synonym of *Watznaueria*. *Cyclagelosphaera* and *Watznaueria* are closely-related; both have strongly precessing element sutures - those on the distal shield show anti-clockwise precession, while the sutures of the proximal shield precess in the opposite direction (= anticlockwise when viewed from the proximal side). *Apertasphaera* (gen. nov.) has a monocyclic distal shield, and a wide, vacant central opening; this genus is constructed mush more simply than other, typical members of the Watznaueriaceae (and appears to lack V-unit elements), but has a similarly constructed, birefringent distal shield. *Haqius* is probably related to this family, but this genus has a weakly imbricate distal shield, and is only weakly birefringent.

Family **Tubodiscaceae** New Family

Genera - *Manivitella*, *Tubodiscus*.

Type species - *Tubodiscus verenae* Thierstein, 1973 emend. Grün *in* Grün & Allemann, 1975.

Definition - Elliptical placoliths with two narrow shields, both composed of imbricating elements, and a proximal tube cycle (composed of subvertically oriented, slightly imbricating elements) that encloses a wide central opening.

Remarks - These two genera are closely-related and, indeed, are difficult to distinguish on the SEM; they are more readily differentiated (as are the various species of *Tubodiscus*) on the LM. Applegate & Bergen (1988) conducted a thorough "same specimen" study of these forms. On the SEM the only discernible difference between *Manivitella* and *Tubodiscus* is in the height and inclination of the proximal extension of the tube cycle (= collar). This collar extends from the smaller, concave shield and is thus located proximally, not distally as assumed by most previous authors (Grün & Allemann, 1975, recognised this fact and amended the genus *Tubodiscus* accordingly). All the species assigned to these genera have similarly constructed rims - the elements of both shields are dextrally imbricate; those on the distal shield are arranged radially, while the proximal cycle of elements have clockwise precessing sutures. This arrangement is very different to the Watznaueriaceae, despite the obvious relationship between these families. These genera are so similar that *Tubodiscus* might reasonably be regarded as a junior synonym of *Manivitella*, but the most highly developed forms of *Tubodiscus* (*T.verenae*) are so distinctive that this genus is retained.

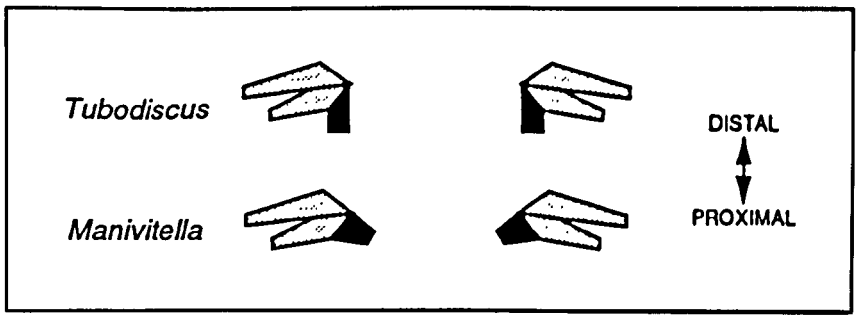


Fig. 2.6 - Schematic cross sections illustrating differentiation of *Tubodiscus* and *Manivitella*.

Family Arkhangelskiellaceae Bukry, 1969

Genera - *Acaenolithus*, *Arkhangelskiella*, *Broinsonia*, *Crucicribrum*, *Gartnerago*, *Kamptnerius*, *Thiersteinia* (+ *Umbria?*).

Description - Placoliths with three or more closely-appressed shields.

Remarks - This is a mid-Upper Cretaceous family; the Tithonian-Berriasian genus, *Umbria* Bralower *et al.*, 1989, is almost certainly not related to later forms, and is only tentatively retained in this family (it is not known in lateral view). *Gartnerago* and *Kamptnerius* have a very similar, light-microscopically distinct rim structure; the other genera are distinguished largely by their central structures, and remain quite unsatisfactorily defined. It is possible that *Acaenolithus* (the earliest definite arkhangelskiellacean) may have evolved from *Diloma* by the rearrangement of its wall cycles to form a placolith rim - these forms certainly appear similar on the LM.

Family Calyptrosphaeraceae Boudreaux & Hay, 1969

Genera - *Calculites*, *Lucianorhabdus*, *Metadoga*, *Zebrashapka* and numerous other genera of dubious distinction proposed for Upper Cretaceous species (see Perch-Nielsen, 1985).

Description - Holococcoliths, composed of many uniformly-sized calcite microcrystals (rather than having specialised elements of differing size and shape, as in heterococcoliths).

Remarks - Certain modern coccolithophores are known to produce both holo- and heterococcoliths, at different stages in their life cycles, so this is a strictly morphological group that probably includes forms conspecific with various heterococcolith species. Fossil holococcoliths are very often recrystallised and/or overgrown, and may not be discernibly microcrystalline on the SEM. They are often divided into a few large blocks, or segments, giving distinctive LM extinction patterns.

Family Braarudosphaeraceae Deflandre, 1947

Genera - *Braarudosphaera, Bukryaster, Micrantholithus, Trapezopentus.*
Description - Nannoliths constructed from five non-imbricating, jointive segments.
Remarks - The various, easily recognised species are defined according to the geometry of their segments. The distinction between *Micrantholithus* and *Braarudosphaera* is slightly blurred (see discussion under *Micrantholithus*). Pentalith is a useful descriptive term that is applied exclusively to these forms (meaning the whole nannolith, not a constituent segment). The pentaliths of the living species *Braarudosphaera bigelowii* interlock in such a way that the cell is completely sealed from its external environment; this suggests that the "coccosphere" is really a resting stage or cyst. Lambert (1986) reported similar "coccospheres" of *Braarudosphaera* in the Albian. However, the pentaliths of *Micrantholithus* could not possibly interlock in this way. The eight-rayed genus *Kokia* is probably related to this family (Van Niel, 1994).

Family Ceratolithaceae Norris, 1965

Genera - *Amaurolithus, Angulolithina, Ceratolithus, Ceratolithina, Triquetrorhabdulus.*
Description - Elongate or horseshoe-shaped nannoliths, generally possessing a vertically raised "keel" (giving an essentially triradiate cross-section).
Remarks - This is an essentially Neogene family, with no apparent links to Early Cretaceous forms (*Ceratolithina* spp. and *Triquetrorhabdulus shetlandensis*). *Ceratolithina* is less obviously triradiate than *Triquetrorhabdulus*, but these large and birefringent forms are likely related (see discussion under *Triquetrorhabdulus*). The Late Cretaceous genus *Ceratolithoides* is probably unrelated.

Family Microrhabdulaceae Deflandre, 1963

Genera - *Lithraphidites, Microrhabdulus, Rhabdophidites.*
Description - Elongate, rod-like nannofossils with a cruciform or circular cross-section.
Remarks - *Rhabdophidites* (as amended herein) is applied to rod-like nannofossils with a murolith rim at one end; the similarity of these forms to *Lithraphidites* suggests a coccolithophorid origin for these nannoliths. Thus, this is not strictly a nannolith group.

Family Nannoconaceae Deflandre, 1959

Genera - *Nannoconus, Faviconus.*
Description - Approximately conical nannoliths composed entirely of stacked plates, enclosing an axial cavity or canal.

Remarks - *Nannoconus* contains some 60 species, with no direct resemblance to any other genus, save its monospecific precursor, *Faviconus*. *Faviconus* Bralower (*in* Bralower, *et al.*, 1989) differs from *Nannoconus* in consisting of several stacks of plates that are not arranged in regular spiral fashion.

Family Polycyclolithaceae Forchheimer, 1972 emend. Varol, 1992

Genera - *Eprolithus, Farhania, Lithastrinus, Quadrum, Radiolithus, Uniplanarius* (& *Rucinolithus?*).

Description - Nannoliths consisting of two vertically appressed wall cycles (each composed of the same number of similarly arranged elements), with or without a central diaphragm at their juncture.

Remarks - Varol (1992) provides a thorough reappraisal of this previously chaotically classified group. This family contains a diverse array of forms, but most are quite clearly related (see lineages in Varol, 1992). *Rucinolithus* is here tentatively assigned to this family, based on the bicyclic construction of *Rucinolithus windleyae* (sp. nov.); previously described species of *Rucinolithus* (mostly older) are not discernibly bicyclic, and this species may provide an evolutionary link between these and later, fully-formed polycyclolithaceans (the unequal development of its two cycles perhaps supports this hypothesis).

Incertae sedis genera

It is inevitable that a number of transitional or aberrant forms will not fit into any classification; this is especially likely with nannofossils, since many genera are of uncertain biological affinity. The following genera are currently unassignable, but possible affinities are suggested.

Assipetra - possibly ancestral to some polyclolithaceans.
Clepsilithus - superficially resembles members of the Stephanolithiaceae, but has a strongly imbricating outer wall.
Conusphaera - a very high-walled murolith.
Hayesites - possible polycyclolithacean affinities.
Helicolithus - probably related to *Tranolithus*, and thus to the Chiastozygaceae.
Kokia - probably related to the Braarudosphaeraceae (van Niel, 1994).
Laguncula - probably related to the Rhagodiscaceae.
Lapideacassis - murolith-like construction (or of non-coccolithophorid origin?).
Loxolithus - a simple imbricating murolith (that typifies the "loxolith" rim construction) with chiastozygacean affinities; its lack of any central structure precludes assignment to this family.

Percivalia - probably related to the Rhagodiscaceae.
Pickelhaube - aberrant form, almost certainly related to the Cretarhabdaceae.
Prediscosphaera - probably related to the Biscutaceae.
Repagulum - possibly related to the Cretarhabdaceae.
Tegumentum - probably related to the Chiastozygaceae.
Tranolithus - probably related to the Chiastozygaceae.
Tegulalithus - only superficially resembles the Nannoconaceae and Polycyclolithaceae.

2.4 - SYSTEMATIC PALAEONTOLOGY

Rationale and conventions applied in the following section

Taxa are treated in alphabetical order to facilitate location. Taxonomic descriptions and remarks have been limited to those species that are new / ill-defined / especially important (biostratigraphically / palaeoceanographically), but since many species are still poorly defined, a relatively large number are discussed in detail.

Ideally, every new species should be illustrated by means of the "same specimen" or "specimen transfer" technique, whereby a single, holotypic specimen is photographed on both the LM and SEM. However, this technique is time consuming and often yields disappointing results, since what appears on the LM to be a perfect specimen is often found to be covered by overgowth or clay when viewed on the SEM. This study relied on careful selection of samples for SEM work to ensure relocation of the "mystery bugs". Wherever possible each new species is illustrated on both LM and SEM, and in as many different orientations (in both media) as possible. New and previously ill-defined species are illustrated by means of several specimens, to show the consistency (or otherwise) of their form.

Full synonymy lists are not given - a number of junior synonyms and misassignments have been propagated for so long that to list all synonyms would be wasteful of space. The reader is referred to Perch-Nielsen (1985) as a starting point to locate all the synonyms. All referenced illustrations (published or in this study) are qualified by means of the following abbreviations: LM = light micrograph; EM = electron micrograph (scanning or transmission).

Calcareous nannofossils considered in this study (in alphabetical order of generic epithets)

Acaenolithus galloisii Black, 1973
Acaenolithus matalosus (Stover, 1966) comb. nov.
Acaenolithus viriosus Jeremiah, *in press*
Acaenolithus? sp.1
Acaenolithus? sp.2
Apertasphaera jakubowskii sp. nov.
Apertasphaera sp.
Axopodorhabdus dietzmannii (Reinhardt, 1965) Wind & Wise, 1983
Axopodorhabdus albianus (Black, 1967) Wind & Wise in Wise & Wind, 1977
Assipetra infracretacea (Thierstein, 1973) Roth, 1973
Assipetra terebrodentarius (Applegate *et al.* in Covington and Wise, 1987) Rutledge & Bergen in Bergen, 1994
Assipetra sp.1
Biscutum constans (Górka, 1957) Black in Black & Barnes, 1959
Biscutum dissimilis Wind & Wise in Wise & Wind, 1977
Biscutum erismatum (Wind & Wise, 1977) Grün & Zweili, 1980
Braarudosphaera africana Stradner, 1961
Braarudosphaera batiliformis Troelsen & Quadros, 1971
Braarudosphaera bigelowii (Gran & Braarud, 1935) Deflandre, 1947
Braarudosphaera discula Bramlette & Riedel, 1954
Bukrylithus ambiguus Black, 1971
Calcicalathina oblongata (Worsley, 1973) Thierstein, 1976
Calculites burnettiae sp. nov.
Calculites? sp.1
Ceratolithina bicornuta Perch-Nielsen, 1988
Ceratolithina cruxii Perch-Nielsen, 1988
Ceratolithina hamata Martini, 1967
Chiastozygus sp.1
Chiastozygus sp.2
Chiastozygus sp.3
Chiastozygus sp.4
Clepsilithus maculosus sp. nov.
Conusphaera rothii (Thierstein, 1971) Jakubowski, 1986
Corollithion achylosum (Stover, 1966) Thierstein, 1971
Corollithion protosignum (Worsley, 1971) comb. nov.
Cretarhabdus angustiforatus (Black, 1971) Bukry, 1973
Cretarhabdus conicus Bramlette & Martini, 1964

Cretarhabdus inequalis Crux, 1987
Cretarhabdus madingleyensis (Black, 1968) Crux, 1989
Cretarhabdus octofenestratus Bralower in Bralower *et al.*, 1989
Cretarhabdus radiatus (Worsley, 1971) comb. nov.
Cretarhabdus schizobrachiatus (Gartner, 1968) Bukry, 1969
Cretarhabdus striatus (Stradner, 1963) Black, 1973
Cretarhabdus surirellus (Deflandre, 1954) Reinhardt, 1970
Crucibiscutum hayi (Black, 1973) Jakubowski, 1986
Crucibiscutum pinnatus (Black, 1971) comb. nov.
Crucibiscutum salebrosum (Black, 1971) Jakubowski, 1986
Crucibiscutum sp. cf. *C.salebrosum*
Crucicribrum erraticum (Stover, 1966) comb. nov.
Cruciellipsis cuvillieri (Manivit, 1966) Thierstein, 1971
Cyclagelosphaera argoensis Bown, 1992
Cyclagelosphaera brezae Applegate & Bergen, 1988
Cyclagelosphaera deflandrei Manivit, 1966
Cyclagelosphaera margerelii Noël, 1965
Cyclagelosphaera rotaclypeata Bukry, 1969
Cyclagelosphaera papilla sp. nov.
Diadorhombus rectus Worsley, 1971
Diloma galiciense Bergen, 1994
Diloma primitiva (Worsley, 1971) Wind & Cepek, 1979
Diloma? sp.1
Diloma? sp.2
Discorhabdus ignotus (Górka, 1957) Perch-Nielsen, 1968
Eiffellithus monechiae Crux, 1991
Eiffellithus striatus (Black, 1971) Applegate & Bergen, 1988
Eiffellithus turriseiffelii (Deflandre in Deflandre & Fert, 1954) Reinhardt, 1965
Eiffellithus windii Applegate & Bergen, 1988
Eiffellithus sp.1
Ethmorhabdus hauterivianus Black, 1971
Eprolithus floralis (Stradner, 1961) Stover, 1966
Farhania varolii (Jakubowski, 1986) Varol, 1992
Flabellites oblongus (Bukry, 1969) Crux, 1982
Gartnerago nanum Thierstein, 1974
Gartnerago praeobliquum Jakubowski, 1986
Gartnerago theta (Black, 1959) Jakubowski, 1986
Gaarderella granulifera Black,1973
Grantarhabdus meddii Black, 1971
Grantarhabdus coronadventis (Reinhardt, 1966) Grün in Grün & Allemann, 1975

Haqius circumradiatus (Stover, 1966) Roth, 1978
Haqius ellipticus (Grün, 1975) Bown, 1992
Hayesites irregularis (Thierstein, 1972) Applegate *et al.* in Covington & Wise, 1987
Helenea chiastia Worsley, 1971
Helenea conus (Worsley, 1971) comb. nov.
Helenea quadrata (Worsley, 1971) comb. nov.
Helenea staurolithina Worsley, 1971
Helicolithus trabeculatus (Górka, 1957) Verbeek, 1977
Hemipodorhabdus gorkae (Reinhardt, 1969) Grün in Grün & Allemann, 1975
Kokia borealis Perch-Nielsen, 1988
Kokia curvata Perch-Nielsen, 1988
Laguncula boletiformis (Black, 1972) comb. nov.
Lapideacassis glans Black, 1971
Lapideacassis mariae Black, 1971
Lithraphidites bollii (Thierstein, 1971) Thierstein, 1973
Lithraphidites carniolensis Deflandre, 1963
Lithraphidites moray-firthensis Jakubowski, 1986
Lithraphidites pseudoquadratus Crux, 1981
Loxolithus armilla (Black in Black & Barnes, 1959) Noël, 1965
Manivitella pemmatoidea (Deflandre in Manivit, 1965) Thierstein, 1971
Markalius inversus (Deflandre in Deflandre & Fert, 1954) Bramlette & Martini, 1964
Markalius? sp.
Micrantholithus brevis Jakubowski, 1986
Micrantholithus hoschulzii (Reinhardt, 1966) Thierstein, 1971
Micrantholithus obtusus Stradner, 1963
Micrantholithus speetonensis Perch-Nielsen, 1979
Micrantholithus sp.1
Micrascidites? sp.
Monniotia? sp.
Nannoconus abundans Stradner & Grün, 1973
Nannoconus borealis Perch-Nielsen, 1979
    var.A
    var.B
Nannoconus bucheri Brönnimann, 1955
Nannoconus circularis Deres & Achéritéguy, 1980
Nannoconus cornuta Deres & Achéritéguy, 1980
Nannoconus elongatus Brönnimann, 1955
Nannoconus globulus Brönnimann, 1955
Nannoconus inconspicuous Deflandre & Deflandre-Rigaud, 1962
Nannoconus inornatus sp. nov.

Nannoconus kamptneri Brönnimann, 1955
Nannoconus multicadus Deflandre & Deflandre-Rigaud, 1960
Nannoconus oviformis Perch-Nielsen, 1988
Nannoconus pseudoseptentrionalis sp. nov.
Nannoconus steinmannii Kamptner, 1931
Nannoconus truitti Brönnimann, 1955
Nannoconus wassallii Brönnimann, 1955
Nannoconus sp. (short, biflanged)
Nannoconus sp. (tall, biflanged)
Nannoconus sp. (weakly birefringent disk)
Neoparhabdolithus stubbingsii (Black, 1971) comb. nov.
Neoparhabdolithus sp.1
Octocyclus reinhardtii (Bukry, 1969) Wind & Wise, 1977
Percivalia fenestrata (Worsley, 1971) Wise, 1983
Perissocyclus fletcheri Black, 1971
Perissocyclus noelae Black, 1971
Perissocyclus plethotretus (Wind & Cepek, 1979) Crux, 1989.
Perissocyclus tayloriae Crux, 1989.
Pickelhaube furtiva (Roth, 1983) Applegate *et al.* in Covington & Wise, 1987
Prediscosphaera columnata (Stover, 1966) Perch-Nielsen, 1984
Prediscosphaera spinosa (Bramlette & Martini, 1964) Gartner, 1968
Radiolithus antiquus (Perch-Nielsen, 1979) comb. nov.
Radiolithus orbiculatus (Forchheimer, 1972) Varol, 1992
Radiolithus planus Stover, 1966
Repagulum parvidentatum (Deflandre & Fert, 1954) Forchheimer, 1972
Rhabdophidites parallelus (Wind & Cepek, 1979) Lambert, 1987
Rhabdophidites pseudocarinolithus (Applegate & Bergen, 1988) comb. nov.
Rhagodiscus achlyostaurion (Hill, 1976) comb. nov.
Rhagodiscus angustus (Stradner, 1963) Reinhardt, 1971
    subsp. *angustus*
    subsp. *parvus* nov. subsp.
Rhagodiscus asper (Stradner, 1963) Reinhardt, 1967
Rhagodiscus cepekii (Crux, 1987) comb. nov.
Rhagodiscus fenestratus (Stover, 1966) comb. nov.
Rhagodiscus infinitus (Worsley, 1971) Applegate *et al.* in Covington & Wise, 1987
Rhagodiscus nebulosus Bralower *et al.*, 1989
Rhagodiscus pseudoangustus Crux, 1987
    var.1
    var.2
Rhagodiscus reniformis Perch-Nielsen, 1973

Rhagodiscus splendens (Deflandre, 1953) Verbeek, 1977
Rotelapillus laffittei (Noël, 1957) Noël, 1973
Rucinolithus windleyae sp. nov.
Scapholithus brasiliensis (Bukry, 1969) comb. nov.
Scapholithus fossilis Deflandre in Deflandre & Fert, 1954
Seribiscutum primitivum (Thierstein, 1974) Filewicz *et al.* in Wise & Wind, 1977
Sollasites arcuatus Black, 1971
Sollasites horticus (Stradner *et al.* in Stradner & Adamiker, 1966) Cepek & Hay, 1969
Sollasites lowei (Bukry, 1969) Roth, 1970
Stradnerlithus geometricus (Górka, 1957) Bown & Cooper, 1989
Stradnerlithus hexserratus (Worsley, 1971) comb. nov.
Stradnerlithus rhombicus (Stradner & Adamiker, 1966) Bukry, 1969
Stradnerlithus silvaradius (Filewicz *et al.* in Wind & Wise, 1977) Rahman & Roth, 1991
Speetonia colligata Black, 1971
Staurolithites angustus (Stover, 1966) Crux, 1991
Staurolithites crux (Deflandre in Deflandre & Fert, 1954) Caratini, 1963
Staurolithites dibrachiata (Gartner, 1968) comb. nov.
Staurolithites elliptica (Gartner, 1968) Bukry, 1969
Staurolithites gausorhethium (Hill, 1976) comb. nov.
Staurolithites? glabra Jeremiah, *in press*
Staurolithites mitcheneri (Applegate & Bergen, 1988) comb. nov.
Staurolithites mutterlosei Crux, 1989
Staurolithites sp.1
Stephanolithion atmetros Cooper, 1987
Tegumentum bergeni sp. nov.
    var. *bergeni*
    var. *minor*
    var. *quasioctiformis*
Tegumentum octiformis (Köthe, 1981) Crux, 1989
Tegumentum stradneri Thierstein in Roth & Thierstein, 1972
Tegulalithus septentrionalis (Stradner, 1963) Crux, 1986
    var.A
    var.B
Tetrapodorhabdus decorus (Deflandre, 1954) Wind & Wise in Wise & Wind, 1977
Tranolithus gabalus Stover, 1966
Tranolithus orionatus Reinhardt, 1966
Tranolithus sp.
Trapezopentus sarmatus Wind & Cepek, 1979
Triquetrorhabdulus shetlandensis Perch-Nielsen, 1988
Triquetrorhabdulus? sp.1

Tubodiscus jurapelagicus (Worsley, 1971) Roth, 1973
Tubodiscus parvus sp. nov.
Tubodiscus verenae Thierstein, 1973
Watznaueria barnesae (Black in Black & Barnes, 1959) Perch-Nielsen, 1968
Watznaueria biporta Bukry, 1969
Watznaueria britannica Stradner, 1963
Watznaueria communis Reinhardt, 1964
Watznaueria fasciata Wind & Cepek, 1979
Watznaueria fossacincta (Black, 1971) Bown in Bown & Cooper, 1989
Watznaueria ovata Bukry, 1969
Watznaueria rawsonii Crux, 1987
Zebrashapka vanhintei Covington & Wise, 1987
Zeugrhabdotus compactus (Bukry, 1969) comb. nov.
Zeugrhabdotus diplogrammus (Deflandre in Deflandre & Fert, 1954) comb. nov.
Zeugrhabdotus "elegans" (Gartner, 1968) comb. nov.
Zeugrhabdotus embergeri (Noël, 1959) Perch-Nielsen, 1984
Zeugrhabdotus erectus (Deflandre in Deflandre & Fert, 1954) Reinhardt, 1965
Zeugrhabdotus sp. cf. *Z.erectus*
Zeugrhabdotus noeliae Rood *et al.*, 1971
Zeugrhabdotus scutula (Bergen, 1994) comb. nov.
Zeugrhabdotus sp. cf. *Z.scutula*
Zeugrhabdotus spiralis (Bramlette & Martini, 1964) comb. nov.
Zeugrhabdotus trivectis Bergen, 1994
Zeugrhabdotus xenotus (Stover, 1966) comb. nov.
Spicule sp.1
Spicule sp.2

Genus *Acaenolithus* Black, 1973

Remarks - Black (1973, p.57) described this genus as "in most respects resembling *Broinsonia* Bukry, 1969, but differing in the presence of a knob or spine". This may seem a dubious criterion for generic subdivision, but it seems that all early arkhangelskiellaceans with a central cross have a distal process, which is often prominent, and it is probably worth setting them apart from spineless later forms. However, this said, there comes a point in the mid-Cretaceous when it is virtually impossible to distinguish *Acaenolithus* and *Broinsonia*, and so *Acaenolithus* might reasonably be regarded as a junior synonym of *Broinsonia* (Bukry, 1969).

Acaenolithus matalosus (Stover, 1966) comb. nov.

1966 *Coccolithus matalosus* Stover, p.139, pl.2, fig.1 (LM), *non* fig.2; pl.8, fig.10.
1972 *Broinsonia signata* (Noël, 1969) Noël, 1970; Roth & Thierstein, p.479, pl.13, figs.12-20; p.481, pl.14, figs.1-5 (EM & LM; same specimen).
1976 *Broinsonia dentata* Bukry, 1969; Hill, pl.3, figs.1-6 (LM); pl.13, figs.10-11 (EM).
1976 *Vagalapilla matalosa* (Stover, 1966) Thierstein, 1973; Hill, pl.12, figs.7-15 (LM).
1990 *Vagalapilla matalosa* (Stover, 1966) Thierstein, 1973; Mutterlose & Wise, p.350, pl.5, fig.4-7 (EM & LM).

Remarks - This species has caused a considerable amount of chaos. Stover's holotype (from the Lower Cenomanian) is clearly a placolith, with a spine-bearing axial cross, and even though Stover described it as having only "two closely appressed plates (= shields)" it is clearly assignable to *Acaenolithus* (the multiple tiers of the rim could not be discerned on the LM). The paratype, however, is a murolith (with a marginal wall), and has recently been named as *Staurolithites glabra* by Jeremiah (*in press*); Bergen (1994) also differentiated these two forms, assigning the paratype to *Vagalapilla* sp.A. Cepek & Hay (1969) and Thierstein (1973) had the paratype in mind when they reassigned this species to *Staurolithites matalosus* and *Vagalapilla matalosa*, respectively. However, they did not formally emend Stover's description, and anyway the holotype could not possibly be amended to include such forms. Recent authors have tended to use *Vagalapilla matalosa* for one or other, or even both of these forms, resulting in a good deal of confusion. Crux (1989) and Mutterlose (1991) used the first occurrence of *Vagalapilla matalosa* as a late Barremian zonal marker; these authors likely had a composite concept of this species, including several small to medium-sized forms here assigned to *Acaenolithus*. *Vagalapilla matalosa* has also been applied to Valanginian-Hauterivian forms from the Argo Abyssal Plain (Bown, 1992; Mutterlose, 1992); these forms are remarkably similar to the *matalosus* holotype, but their relationship is uncertain and unlikely to have been direct (their SEM ultrastructure is unknown). The distinction between *A.matalosus* and

Broinsonia dentata/Broinsonia signata is unclear and, in any case, it is doubtful whether *B.dentata* and *B.signata* can be reliably differentiated on the LM. In well-preserved material the "teeth" of *dentata* types can occasionally be discerned in phase contrast. The holotype of *matalosus* shows signs of these teeth. Thus, both *B.dentata* and *B.signata* should, strictly speaking, be regarded as junior synonyms of *matalosus*, for LM purposes. Similarly, the various species of *Acaenolithus* and *Cribricatillus* described by Black (1973) might, for LM purposes, be regarded as synonymous with *A./B.matalosus/a.*

The concept of *A.matalosus* is limited herein to large, robust, Late Cretaceous forms, as typified by Stover's holotype. Such forms, which are generally assigned to *Broinsonia signata* by other authors, have not been recorded in this study. Instead, a number of species of *Acaenolithus* have been distinguished; several of these could not be reconciled with Black's holotypic SEMs and are thus recorded as "sp.".

Acaenolithus viriosus Jeremiah, *in press*

Plate 2, Fig. 19 (LM).

Differentiation - This form is readily differentiated from other species of *Acaenolithus/Broinsonia* on the LM by its large size (>9μm long), wide central openings, medianly-split cross-bars, and prominent spine. The prominent spine allows it to be assigned to *Acaenolithus* with certainty. This species differs from similarly large, Upper Cretaceous forms (herein assigned to *A.matalosus*) in having much wider central openings, and a prominent spine.

Occurrence - Fairly common in the Lower Albian of the Heslerton Borehole. This is a useful marker species - Jeremiah (*in press*) found it to be restricted to the Lower Albian of the North Sea area. Bergen (1994) probably included this species in his concept of *Broinsonia* sp. (= *A.matalosus*), whose first occurrence he recorded in the basal Albian of the Vocontian Trough.

Acaenolithus ?galloisii Black, 1973

Plate 2, Fig. 18 (LM).

Description (LM) - Medium-sized (5-7μm long) form with a wide, broadly elliptical rim. A thick axial cross is discernibly fibrous in cross-polarised light and appears split in some orientations. A short spine-base may be visible.

Remarks - Following Jeremiah (*in press*), these medium-sized, relatively compact forms are tentatively assigned to *A.galloisii*, although they are light-microscopically

indistinguishable from Upper Cretaceous forms commonly assigned to *Broinsonia signata*. Thus, as far as light-microscopists are concerned, this is a long-ranging (Aptian-?Campanian) morphotype.

Acaenolithus? sp.1

Plate 2, Fig. 16 (LM).

Description (LM) - Medium-sized (6-7μm long) form with a relatively narrow rim, delicate axial cross, and consequently wide central openings. The central area is diamond-shaped, and the cross-bars are parallel-sided and unstriate.

Differentiation - This species is altogether more delicately constructed than *A.galloisii* or *A.viriosus*, and lacks the medianly-split cross-bars of these species. It is larger and more openly constructed than *Acaenolithus?* sp.2. It is very similar to *Diloma?* sp.1 and *Diloma?* sp.2 (both of which appear considerably earlier); the only discernible difference is in the outline of the central area - this is elliptical in *Diloma?* sp.1 and sp.2, but diamond-shaped in *Acaenolithus?* sp.1.

Remarks - This species was probably the major constituent of the *"Vagalapilla matalosa"* (composite concept) of Crux (1989) and Mutterlose (1991). These authors used the first occurrence of *"V.matalosa"* to define a late Barremian zonal boundary. Neither author recorded the very similar, and earlier appearing *Diloma?* sp.1 or *Diloma?* sp.2 (nor, indeed, did they record any species of *Diloma*). These similar forms rather detract from the biostratigraphical utility of this species.

Occurrence - This ancestral form of *Acaenolithus* seems restricted to the Late Barremian. It is recorded in the Upper Cement Beds of Speeton (*?stolleyi* Zone), the *?germanica* Zone of Germany, and the lower part of the Heslerton Borehole (*?bidentatum* Zone).

Acaenolithus? sp.2

Plate 2, Fig. 17 (LM).

Description (LM) - Small (3-4μm long), compact form with a relatively wide rim, diamond-shaped central area and simple (unstriate) axial cross.

Differentiation - This form is differentiated from the light-microscopically similar *Acaenolithus?* sp.1, *Diloma?* sp.1 and *Diloma?* sp.2 by its smaller size and more compact form (with relatively narrow central openings). It is smaller than *A.galloisii* and lacks the striate cross-bars of that species.

Remarks - Crux (1989) and Mutterlose (1991) probably included this form in *Vagalapilla matalosa*, whose first occurrence they used to define a zonal boundary.

Occurrence - Upper Barremian to Albian of England and Germany; common in the Aptian-Albian. This species is particularly common in the basal Atherfield Clay (Early Aptian). It was recorded rarely in the mid-Hauterivian of Borehole 81/43; contamination is thought unlikely so it may have originated considerably earlier.

Genus *Apertasphaera* gen. nov.

(type species: *Apertasphaera jakubowskii* sp. nov.)

Derivation of name - Latin, *apertus* meaning open, referring to the open central area.
Diagnosis - Modified watznaueriacean placolith with a monocyclic distal shield, and a wide, vacant, central opening (without any inner tube cycle(s)).
Differentiation - *Apertasphaera* differs from *Diazomatolithus* Noël (1965) in having an imbricate, watznaueriacean distal shield, and differs from *Ansulasphaera* Grün & Zweili (1980) in having a monocyclic distal shield (without an inner distal shield cycle) and a much less extended (less tube-like) proximal shield. It differs from most species of *Cyclagelosphaera* and *Watznaueria* (and *Ellipsagelosphaera*, which is considered a junior synonym of the latter genus) in lacking a penetrative V-unit cycle (expressed as an additional, inner cycle of elements visible on the distal shield in *Watznaueria*) and an inner tube cycle. *Apertasphaera* differs from those remaining, aberrant members of the Watznaueriaceae (e.g. *Cyclagelosphaera papilla*) in having an open central area.
Remarks - The type species, *A.jakubowskii* (sp. nov.), has previously been misassigned to *Diazomatolithus lehmanii* Noël (1965). Noël's original description (1965) of *D.lehmanii*, the type species of that genus, was vague, and her Oxfordian holotype was misoriented. Grün (in Grün & Allemann, 1975) subsequently described another species of *Diazomatolithus* (*D.subbeticus*) from the Berriasian. Both *D.lehmanii* and *D.subbeticus* have non-imbricate, monocyclic shields, and lack any additional, inner element cycles; they differ in the height, form, and precession of sutures on their distal shields. Grün & Zweili (1980) erected the genus *Ansulasphaera* to include an unusually formed watznaueriacean coccolith, *A.helvetica*; this species, described from the Callovian, has a typically watznaueriacean distal shield (complete with inner distal shield cycle) but its proximal shield is peculiarly extended to form a tube. Rahman & Roth (1991) described a second species of *Ansulasphaera*, *A.bownii*, from the Upper Kimmeridgian; this differs from *A.helvetica* in having a monocyclic distal shield, and a much shorter, less tube-like, proximal shield. *Apertasphaera jakubowskii* (sp. nov.) seems related to *A.bownii*; both are biconcave in profile, with monocyclic shields, the larger of which (distal) is dextrally imbricate. These two species may, however, be more closely related to *Diazomatolithus* (which has monocyclic shields) than to *A.helvetica* (which has a bicyclic distal shield, and an aberrant proximal shield). Thus, a new genus is erected for these rather unusual watznaueriaceans. The mid-late Cretaceous genus

Cylindralithus Bramlette & Martini (1964) has a tube-like extension, rather similar to *Ansulasphaera*, but this aberrant placolith genus bears little resemblance to the Watznaueriaceae.

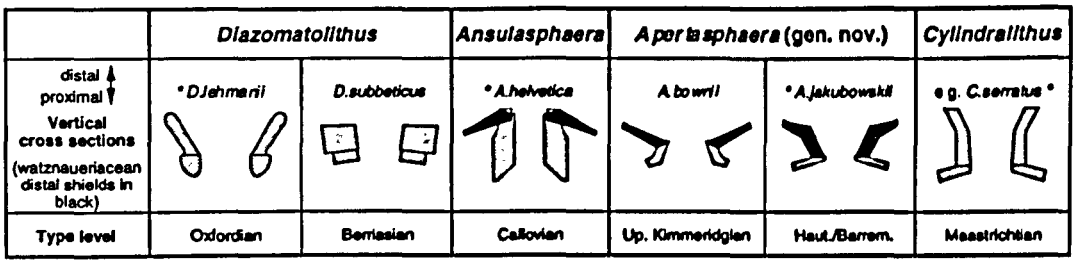


Fig. 2.7 - Key features and differentiation of conical placolith genera (Upper Jurassic - Cretaceous). Type species are asterisked. Watznaueriacean distal shields (dextrally imbricate) are shaded black.

Apertasphaera bownii (Rahman & Roth, 1991) comb. nov.

1991 *Ansulasphaera bownii* Rahman & Roth, p.774, pl.1, figs.9-13; pl.2, fig.1; pl.4, fig.4 (EM & LM).

Remarks - This Upper Jurassic species may have been ancestral to *Apertasphaera jakubowskii* - it is certainly more similar to this species than to *Ansulasphaera helvetica* (the type, and only remaining species of *Ansulasphaera*).

Apertasphaera jakubowskii sp. nov.

Plate 12, Figs. 10-14 (EM);
Plate 9, Fig. 13 (LM).

1982 *Diazomatolithus lehmanii* Noël, 1965; Taylor, pl.4.6, figs.1-2 (EM).
1985 *Diazomatolithus lehmanii* Noël, 1965; Perch-Nielsen, Fig.33.19-20 (EM).
1987 *Diazomatolithus lehmanii* Noël, 1965; Jakubowski, pl.3, figs.13-14 (LM).
1987 *Diazomatolithus lehmanii* Noël, 1965; Thomsen, pl.3, figs.12-14 (EM).
1987 *Diazomatolithus lehmanii* Noël, 1965; Covington & Wise, pl.8, figs.6-7 (EM).
1988 *Diazomatolithus lehmanii* Noël, 1965; Applegate & Bergen, pl.6, fig.9 (EM).
1989 *Diazomatolithus lehmanii* Noël, 1965; Crux, pl.8.10, figs. 1-5 (LM); ?pl.8.2, fig.7 (EM); *non* pl.8.2, fig.10 (EM).
1991 *Diazomatolithus lehmanii* Noël, 1965; Mutterlose, pl.3, figs.1-3 (EM).

Derivation of name - Named in honour of Martin Jakubowski (Shell), for his contributions to Lower Cretaceous nannofossil biostratigraphy.

Diagnosis - Circular to subcircular watznaueriacean placolith, with a monocylic distal shield that is vertically extended in the form of a funnel. The monocyclic shields enclose a vacant central area; there are no additional element cycles.

Description (SEM) - Medium-sized (4-5.5μm diameter) circular (or, possibly, very broadly elliptical) placolith, with a wide, circular, central opening (c.1/3 the diameter of the distal shield). Both proximal and distal shields are monocyclic and no other, internal element cycles are present. The wider, distal shield is composed of 22-30 elements; this shield appears typically watznaueriacean in plan, distal view (the elements are dextrally imbricate, with anticlockwise precessing sutures), but extends proximally to form a low funnel. The extended, funnel-like part of the distal shield joins the inner margin of the proximal shield. The proximal shield, which is only slightly smaller in diameter, consists of about 24 tabular elements; these are radially arranged, and non-imbricating. Both proximal and distal shields are concave outwards - the coccolith is thus biconcave, in side view.

Description (LM) - The distal shield is moderately birefringent (white), and flares markedly on focusing distally. The outer margin of the rim appears diffuse and ragged in cross-polarised light; individual elements, with precessing sutures, can be discerned along the margin (the direction of precession depends on the view). This species is often encountered in side view (see Crux, 1989, pl.8.10, fig.5).

Differentiation - *A.jakubowskii* differs from *Apertasphaera bownii* in having an extended distal, rather than proximal, shield (the distal shield of *A.bownii* is composed of flat, rather than incurved, laths). It is further differentiated from *A.bownii* by having a broader proximal shield, with radial (rather than anticlockwise precessing) sutures. It remains to be seen whether these two similar species can be reliably differentiated on the LM. *A.jakubowskii* differs from species of *Diazomatolithus* in having an imbricate, watznaueriacean, distal shield. It differs from other members of the Watznaueriaceae in having a monocyclic distal shield, and a vacant central area.

Known Range - Late Ryazanian to middle Barremian.

Occurrence - Upper Ryazanian to middle Barremian of the studied North Sea sections (rare in the Barents Sea) - highest recorded occurrence in the *denckmanni* ammonite Zone of Speeton, but highest consistent occurrence considerably lower, in the Lower Barremian *fissicostatum* Zone (common to abundant throughout most of the underlying interval). Taylor (1982) recorded the last occurrence of *"Diazomatolithus lehmanii"* in the Lower Barremian, and Jakubowski (1987) found this datum to be a reliable Lower Barremian marker in the Dutch Sector of the North Sea. Applegate & Bergen (1988) recorded the last consistent occurrence of *"D.lehmanii"* in the middle Barremian of the Galicia Margin; later, sporadic occurrences may have been reworked. Covington & Wise (1987) recorded *"D.lehmanii"* consistently up to the Barremian of DSDP Site 603 (western North Atlantic). Other authors have recorded *"D.lehmanii"* considerably higher, possibly due to different species concepts.

Remarks - This species is a prime example of an initial misidentification being propagated throughout the literature. Older, Valanginian, forms seem slightly larger and more thickly constructed than younger Hauterivian-Barremian forms.
Holotype - Plate 12, Fig. 11 (EM).
Isotypes - Plate 12, Figs. 10, 14 (EM).
Type locality & level - Borehole 81/43 (southern North Sea), 18.00m (uppermost Hauterivian or basal Barremian - see discussion in the Biostratigraphy chapter).

Apertasphaera sp.

Plate 12, Figs. 15 & 16 (EM);
Plate 9, Fig. 14 (LM).

Remarks - These delicate, ring-like coccoliths have much narrower shields than *A.jakubowskii* and, apparently, a greater number of elements in their distal shield. They seem to have a range concurrent with that of *A.jakubowskii*, and may be a dissolution product of that species. Nevertheless, they seemed light microscopically distinct, and were recorded separately.

Genus *Assipetra* Roth, 1973

Assipetra infracretacea (Thierstein, 1973) Roth, 1973

Plate 20, Fig. 18 (LM);
Plate 21, Figs. 12-14 (EM & LM).

Remarks - This nannolith is subrectangular in outline and lacks the numerous radial sutures of the globular *A.terebrodentarius.* A V-shaped extinction line divides off a segment at one or both ends of the subrectangular body. The rather non-descript, crystalline nature of *A.infracretacea* makes identification difficult or impossible in heavily overgrown material, but there is no problem in identifying this dissolution resistant species in well-preserved or lightly etched material.

Assipetra terebrodentarius (Applegate *et al.* in Covington & Wise, 1987) Rutledge & Bergen in Bergen, 1994

Plate 20, Fig. 17 (LM);
Plate 21, Figs. 9-11 (EM & LM).

1987 *Rucinolithus terebrodentarius* Applegate *et al.* in Covington & Wise, p.632, pl.17, figs.7-8 (LM); pl.18, figs.5-7 (EM); pl.19, figs.1-4 (EM).

non 1989 *Rucinolithus terebrodentarius* Applegate *et al.* in Covington & Wise, 1987; Bralower *et al.*, pl.VII, figs.4-6 (EM & LM).

Remarks - This species is composed of "about 10 blocky, euhedral interpenetrating elements" (Applegate *et al.* in Covington & Wise, 1987, p.633), and thus belongs to the genus *Assipetra*. *A.terebrodentarius* is distinguished from the closely-related *A.infracretacea* by its globular (rather than subrectangular) outline and numerous radial sutures visible on the LM. It is distinguished from the unrelated but light microscopically similar *Rucinolithus windleyae* (sp. nov.) by its smaller size (4-5μm diameter), more globular form, and less well-developed petalloid habit. It is important that these three species are distinguished, since their ranges are markedly different.

Occurrence - Lowest occurrence in the basal Barremian (?) *variabilis* ammonite Zone of Speeton, and at a corresponding level in Borehole 81/43. Bergen (1994) records this event in the uppermost Hauterivian *angulicostata* ammonite Zone of S.E. France, suggesting that the Hauterivian/Barremian boundary may be placed slightly too high in the Speeton section. This species is common to abundant throughout the *rarocinctum* Zone of Speeton; it disappears in the *fissicostatum* Zone, only to reappear in the Early Aptian of the Heslerton Borehole (Thomsen, 1987, found this species abundantly in the Early Aptian "Fischschiefer" of Helgoland). Judging from the range charts of Applegate & Bergen (1988), this species may have a similarly disjunct distribution at lower latitudes.

Assipetra sp.1

Description (LM) - A small (3-4μm diameter) spherical form of *Assipetra*, with three or four curved radial sutures.

Remarks - Transitional in form between *A.infracretacea* and *A.terebrodentarius*, but quite distinct from both these species. This form has a smoother, more circular outline than *A.terebrodentarius*, with fewer radial sutures. It is unlikely that this represents an end view of *A.infracretacea* since it has a restricted range and is not recorded in other intervals in which *A.infracretacea* is abundant.

Occurrence - This form seems restricted to the Upper Hauterivian - it was only recorded (rarely but consistently) through a 10 metre section of Borehole 81/43, in an interval unexposed at Speeton. Similarly, Bergen (1994) recorded this form in the Upper Hauterivian of Tethys.

Genus *Biscutum* Black in Black & Barnes, 1959

Remarks - Following a recent reappraisal of the Biscutaceae (de Kaenel & Bergen, 1993), there exists considerable uncertainty as to the definition of genera within this family, and the Cretaceous species traditionally assigned to *Biscutum* should possibly be reassigned to *Palaeopontosphaera*. However, the traditional usage of *Biscutum* is retained here. See further remarks under the Biscutaceae (Section 2.3).

Biscutum constans (Górka, 1957) Black in Black & Barnes, 1959

Plate 18, Fig. 10 (EM).

Remarks - *Biscutum ellipticum*, described by Górka in the same paper (1957) and used preferentially by many later authors, is considered synonymous. This species is used for all small, elliptical biscutaceans without any discernible (LM) structure inside their birefringent central tube. These forms show considerable variation in size and in the relative width of the central tube. The smallest forms (c.1.5µm long) are barely discernible on the LM. Most published SEMs of Lower Cretaceous *Biscutum constans/ellipticum* display a short, tubular central process (e.g. Plate 18, Figs. 8 & 9) and should probably be assigned to *Biscutum erismatum* (Wind & Wise, 1977) Grün & Zweili, 1980. This latter species is rarely recorded from the Cretaceous but Thomsen (1987), who used the SEM almost exclusively, found it to be more common than *B.constans* in the Lower Cretaceous of his North Sea sections. *B.constans* has been used as a palaeoceanographical indicator ("high fertility index") by several authors, so it is important to bear in mind that the LM concept of this "species" may be multispecific, since the several constituent species may have had markedly different environmental preferences.

Genus *Braarudosphaera* Deflandre, 1947

Remarks - This genus is not recorded below the Upper Aptian in this study; earlier records by other authors were probably overgrown specimens of *Micrantholithus* (see also *Micrantholithus* sp.1). Lambert (1986) showed that various Albian species of *Braarudosphaera* (*B.africana*, *B.regularis*, *B.stenorheta*, etc.) are conspecific.

Genus *Calculites* Prins & Sissingh in Sissingh, 1977

Remarks - Crux (1987) described *Calculites sarstedensis*, which he believed to be the oldest representative of this genus, from the uppermost Hauterivian/basal Barremian of Germany. He did not, however, provide micrographs of this species in cross-polarised light, in which the various species of *Calculites* are generally differentiated. Crux (1989) reported that *C.sarstedensis* was too inconspicuous to include in his LM abundance

estimates, but recorded "Holococcolith sp.1" from the Ryazanian to Barremian of Speeton and Germany. He illustrated "Holococcolith sp.1" in cross-polarised light, and did not provide a differential diagnosis from *C.sarstedensis*. In the present study, four distinct forms of *Calculites* were recorded on the LM. All these forms are small (3-4μm long) and moderately birefringent (grey-white); they are readily differentiated in cross-polarised light by the arrangement of their extinction gyres, which reflects their mode of construction. One of these forms is clearly identical to Crux's "Holococcolith sp.1". Several other distinctive, block-formed morphotypes show gradational variation. SEM examination of the block-formed types showed them to be much more solidly constructed than *C.sarstedensis*; they appear much less cellular (although this is probably due to diagenetic overgrowth), consist of several discrete blocks, and lack the distal depressions and spine base/boss of this species. They are also restricted to sediments of older age than the horizon from which *C.sarstedensis* was described. Thus it seems that *C.sarstedensis*, which was not recorded in this study, is a delicate, non-birefringent species, which may be entirely unrelated to the species described herein.

Calculites burnettiae sp. nov.

Plate 8, Figs. 11-14 (EM);
Plate 9, Figs. 2-5 (LM).

Derivation of name - Named in honour of Dr. Jackie Burnett, nannopalaeontologist.
Diagnosis - Small elliptical holococcoliths composed of two to four microcrystalline blocks which join along prominent sutures; the surface of the coccolith is otherwise unornamented.
Description - Small (3-4μm long), elliptical coccoliths which exhibit moderate (grey-white) birefringence and are divided into several blocks by prominent sutures that appear as extinction lines in cross-polarised light. The number and relative development of the blocks is variable - three different varieties are recognised on this basis.
Differentiation - Differs from *C.sarstedensis* and from Upper Cretaceous species of *Calculites* in having a relatively unornamented distal surface (i.e. in lacking pits and a central boss). It also differs from *C.sarstedensis* in having a block-formed construction.
Remarks - Three distinct morphotypes assigned to this species (Fig. 2.8) are provisionally given variety status, although they seem to have differing stratigraphical ranges. Further work may show that these varieties warrant separate specific status. Variety A is the longest-ranging and most common type; the holotype is of this type.
Holotype - Plate 9, Fig. 3 (LM).
Isotype - Plate 8, Fig. 11 (EM).
Type locality & level - Borehole 81/43 (southern North Sea), 46.53m (Upper Hauterivian).

Occurrence - Hauterivian of the North Sea area.

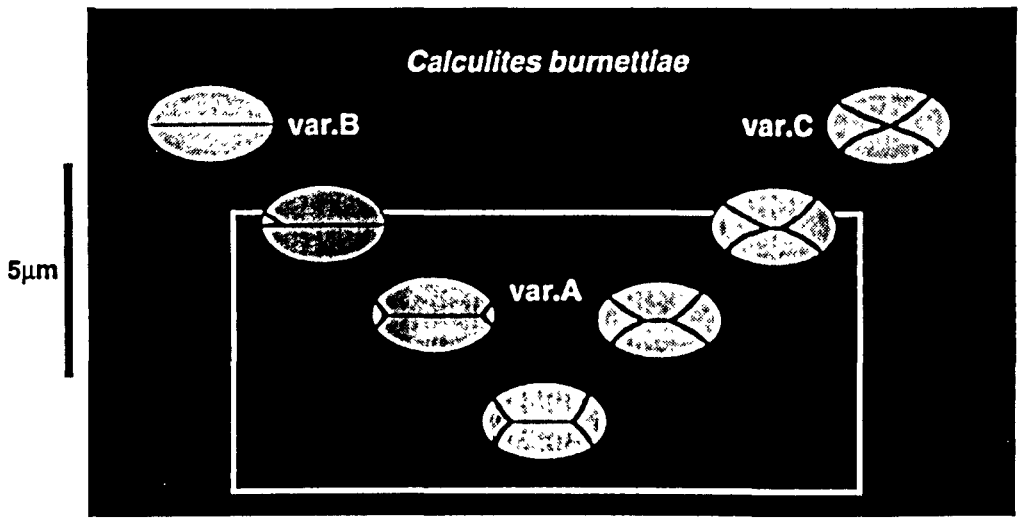


Fig. 2.8 - Light microscopic differentiation of the three varieties of *Calculites burnettiae* (sp. nov.). Their appearance, in cross-polarised light, is largely independant of orientation relative to the polarisers.

Calculites burnettiae var.A

Plate 8, Fig. 11 (EM);
Plate 9, Figs. 2 & 3 (LM).

Diagnosis - Small elliptical holococcolith composed of four blocks, two lateral and two terminal, with the larger lateral blocks joined along a suture in the long axis of the coccolith.

Description (LM) - Small (3-4µm long), elliptical form, of moderate birefringence (grey-white) with a faint longitudinal suture and a prominent V-shaped extinction line at each end. The extinction lines do not change position significantly during rotation of the specimen, and do not meet in the centre of the coccolith, which appears solid.

Description (SEM) - The arrangement of sutures on the distal surface directly reflects the pattern of extinction lines seen on the LM. The surface of the coccolith is otherwise unornamented. All specimens encountered were recrystallised/overgrown, and not very obviously microcrystalline.

Remarks - Forms transitional with variety B, with only rudimentary terminal segments, are fairly common in the Upper Hauterivian.

Occurrence - Lower Hauterivian to Upper Hauterivian (Speeton, Borehole 81/43, and a single record from the Barents Sea); quite sporadic in occurrence, but abundant at certain levels (especially in Borehole 81/43).

Calculites burnettiae var.B

Plate 8, Figs. 13 & 14 (EM);
Plate 9, Fig. 5 (LM).

Diagnosis - Small elliptical holococcolith composed of two blocks that join along a suture lying in the long axis of the coccolith.
Description (LM & SEM) - Small (3-4μm long), elliptical form of moderate birefringence with a faint longitudinal suture, and no other ornament visible in cross-polarised light (no extinction lines are seen). The SEM reveals no more detail - the surface of the coccolith is entirely unadorned by any ornament, save the single, longitudinal suture.
Occurrence - This form seems to have a very limited stratigraphical range - it was only recorded (commonly) in a 4m section of Borehole 81/43, of Late Hauterivian age, and at a corresponding level (*staffi* ammonite Zone) in Germany.

Calculites burnettiae var.C

Fig. 2.8

Description (LM only) - Small elliptical form with prominent extinction gyres which meet at its centre, dividing the coccolith into four segments. This form is very similar to the Upper Cretaceous species *Calculites ovalis.*
Remarks - This form arises from variety A by extension of the terminal segments across the coccolith to meet at its centre. There may be a central perforation at the juncture of the extinction lines, as in Late Cretaceous species.
Occurrence - Restricted to the Upper Hauterivian of Borehole 81/43, where it is was recorded with variety B.

Calculites? sp.1

Plate 9, Fig. 1 (LM).

Holococcolith sp.1 Crux, 1989, p.201, pl.8.10, fig. 35 (LM); non figs. 33-34.

Description (LM only) - Small (3-4μm long), elliptical form, of moderate birefringence (grey-white). Under cross-polarised light, the arrangement of the extinction gyres changes very significantly during rotation of the specimen. A vague central structure (consisting of a central boss, surrounded by a cycle of depressions?) is visible in cross-polarised light. A longitudinal slit is visible under phase contrast.

Remarks - This species differs from *Calculites burnettiae* in having extinction gyres that are not fixed in position and change during rotation of the specimen (thus it does not seem to be block-formed). It also has a more highly ornamented distal surface than *C.burnettiae*. Similar forms are known from the Albian - Hill (1976) misassigned such forms to *Biscutum supracretaceum*, and Jeremiah (*in press*) reports them from the Albian of the U.K.. This form was not differentiated from *Calculites burnettiae* var.A until a late stage in this study, and is included with it on the range charts; likewise, Crux (1989) probably included *Calculites burnettiae* in "Holococcolith sp.1".

Occurrence - Upper Valanginian to Lower Hauterivian of Borehole 81/43 and Speeton (occasionally abundant); forms apparently transitional with *Calculites burnettiae* are observed in the Lower Hauterivian. Crux (1989) recorded "Holococcolith sp.1" down to the Upper Ryazanian of Speeton, but his illustrated Ryazanian specimen probably belongs to a different species (possibly *Markalius?* sp. - see Plate 6, Fig. 21). Crux recorded "Holococcolith sp.1" rarely as high as the Upper Barremian, but these late occurrences were probably small specimens of *Watznaueria communis*, which has a similar appearance in cross-polarised light.

Genus *Chiastozygus* Gartner, 1968

Remarks - Following Thierstein (1971, 1973) a number of authors have used the first occurrence of *Chiastozygus litterarius* ((Górka, 1957) Manivit, 1971) to mark the base of the Aptian. However, due to a lack of detail in the original description (Górka's holotype is a generalised sketch) this species is very poorly defined, and similar forms are known to occur down to the Lower Hauterivian. Unless all forms of *Chiastozygus* are to be lumped into *C.litterarius*, the various species proposed for such forms must be more accurately defined using specimen transfer techniques. This was not undertaken in the present study, and the various light-microscopically distinct morphotypes are numbered sp.1 to sp.4. Black (1971) described *Chiastozygus tenuis* from the Barremian of Speeton, but his holotypic SEM cannot yet be reconciled with the various types observed on the LM.

Chiastozygus sp.1

Plate 4, Fig. 12 (LM).

Remarks - This category is used for the simplest forms of *Chiastozygus*, with simple, unstriate (in cross-polarised light) cross-bars. The rim is relatively narrow and appears unicyclic. This form was first recorded in the basal Hauterivian of Borehole 81/43, and is thus the ancestral form of *Chiastozygus*.

Chiastozygus sp. 2

Plate 4, Fig. 13 (LM).

Remarks - Characterised by a distinctive central cross - the cross-bars appear split along their length in cross-polarised light and are sigmoidally curved to join the rim tangentially (forming a figure of eight). The rim appears uncyclic.
Occurrence - This form seems restricted to the Upper Hauterivian; it is occasionally common within this interval.

Chiastozygus sp.3

Plate 4, Fig. 14 (LM).

Chiastozygus sp.2 Crux, 1989, p.182 (not illustrated).

Remarks - These forms have a simple rim, that is not obviously bicyclic, and straight cross-bars that appear medianly split in cross-polarised light (each bar is divided lengthways into two parts by a straight extinction line).
Occurrence - Upper Hauterivian to Lower Barremian, and again in the Upper Aptian and Albian; the later forms are rather less delicate with broader cross-bars. Crux (1989) recorded the highest occurrence of his *Chiastozygus* sp.2 in the Early Barremian *Aulacoteuthis* belemnite Zone of Germany, seeming to confirm that this "species" has a disjunct distribution. The Aptian-Albian forms are assignable to *Chiastozygus platyrhetus* (Hill, 1976), but because of the likelihood that the Neocomian forms are unrelated they are retained in open nomenclature.

Chiastozygus sp.4

Plate 4, Fig. 15 (LM).

1971 *Chiastozygus litterarius* (Górka, 1957) Manivit, 1971; Thierstein, pl.2, figs.17-21 (EM & LM).
1972 *Chiastozygus litterarius* (Górka, 1957) Manivit, 1971; Roth & Thierstein, p.455, pl.1, figs.1-6 (EM & LM; same specimen).
1976 *Chiastozygus litterarius* (Górka, 1957) Manivit, 1971; Thierstein, p.343, pl.3, figs.31-32 (LM).

Remarks - I have used Thierstein's (1971; 1976; in Roth & Thierstein, 1972) concept of *C.litterarius* for this category, applying it to forms which have a fairly robust, bicyclic

rim composed of two equally birefringent cycles, with relatively thick, birefringent cross-bars which appear fibrous, but are not medianly divided. Such forms were first recorded in the uppermost Barremian of the Heslerton Borehole, in a position approximating Thierstein's supposed datum. However I am not confident that these forms can be reliably differentiated from earlier forms of *Chiastozygus*, especially since diagenetic overgrowth of earlier forms could produce a closely similar form. It is notable that *C.litterarius* was the only species of *Chiastozygus* recorded by Thierstein (1973), in his relatively poorly preserved material; this relatively robust form may have been the only form of *Chiastozygus* to be preserved.

Genus *Clepsilithus* Crux, 1987

Clepsilithus maculosus sp. nov.

Plate 8, Figs. 2, 4 & 5 (EM);
Plate 9, Fig. 7 (LM).

1982 *Stradnerlithus comptus* Black, 1971; Taylor, p.71, pl.4.6, figs.13-14 (EM).
1987 *Stradnerlithus comptus* Black, 1971; Jakubowski, p.117, pl.2, figs.23-24 (LM).
1988 *Thurmanolithion clatratum* Grün & Zweili, 1980; Applegate & Bergen, p.336, pl.17, fig.2 (EM).
1989 *Stradnerlithus comptus* Black, 1971; Crux, p.207, pl.8.13, figs.26-28 (LM).
1991 *Stradnerlithus comptus* Black, 1971; Mutterlose (not illustrated).
1991 *Stradnerlithus comptus* Black, 1971; Bralower, p.430, fig.6.41-42 (LM).

Derivation of name - Latin, *maculosus* meaning spotted; referring to the brightly-spotted appearance of the cycle of central area bars in cross-polarised light.
Diagnosis - Elliptical murolith with a bicyclic wall, the outer cycle of which is dextrally imbricate, and a central area occupied by about 14 short, radially-arranged bars which support a diamond-shaped central platform.
Description (LM & EM) - Small (4-5µm long), elliptical murolith with a bicyclic wall that exhibits a bicyclic interference pattern of contrasting birefringence. The slightly flaring outer wall consists of about 25 dextrally imbricate elements, and is only weakly birefringent (grey). The arrangement of elements in the inner wall cycle is uncertain, but this cycle is brightly birefringent (white). Each of the 12-16 regularly arranged radial bars consists of two laterally fused elements, and exhibits white birefringence; these bars support a rather less birefringent (grey-white), diamond-shaped platform that lies along the long axis of the central area. There is no distal process.
Differentiation - *Stradnerlithus comptus*, which was poorly illustrated by Black (1971, pl.31, fig.10) from the Kimmeridgian, but rather better illustrated by Barnard and

Hay (1974, as *Stradnerlithus dorsetense*) from the Oxfordian, has a similar number of radially arranged bars but these support a slender longitudinal bar, not a diamond-shaped platform as in *C.maculosus*. *S.comptus* also has a narrow, apparently monocyclic wall composed of non-imbricate elements, is altogether much more delicately constructed than *C.maculosus*, and probably has very low relief on the LM (it has not, in fact, been described on the LM). Grün and Zweili (1980, p.331, pl.11, fig.6) illustrate a more robustly constructed Oxfordian specimen of *S.comptus*, but this has been thickened by overgrowth, as has much of their material. *Thurmanolithion clatratum* has a spine-bearing central cross, rather than a central platform, and is altogether differently constructed. *Clepsilithus polystreptus* Crux, 1987, differs from *C.maculosus* in having a less developed inner wall cycle, and fewer central bars (that are differently constructed) but this very small form has not been observed on the LM.

Remarks - This species is very distinctive in cross-polarised light - the bars appear as a cycle of regularly spaced bright spots, and even small fragments can be identified with confidence. The only contemporary species with which *C.maculosus* might be confused is the similarly proportioned *Cretarhabdus inequalis*, but this latter species has a much less regular central structure (see remarks under *C.inequalis*).

Holotype - Plate 8, Fig. 2 (EM).

Isotype - Plate 8, Fig. 5 (EM).

Type locality & level - Borehole 81/43 (southern North Sea), 32.80m (Upper Hauterivian).

Occurrence - Hauterivian of the North Sea area, occurring consistently within the uppermost Hauterivian (above the last occurrence of *Tegulalithus septentrionalis*). The last occurrence of this species provides an excellent approximation of the Hauterivian-Barremian boundary, as currently defined at Speeton.

Genus ***Cretarhabdus*** Bramlette & Martini, 1964

(syn: *Stradneria* Reinhardt, 1964)
(syn: *Polypodorhabdus* Nöel, 1965)
(syn: *Retecapsa* Black, 1971)
(syn: *Cretarhabdella* Black, 1971)
(syn: *Allemanites* Grün in Grün & Allemann, 1975)

Remarks - Numerous genera have been proposed for the forms herein assigned to *Cretarhabdus*, but the generic distinctions are difficult to apply on the SEM and virtually impossible on the LM. More detailed SEM studies may reveal that generic subdivision of this group is warranted, but for the moment it is thought advantageous to unite a wide array of light-microscopically similar forms under *Cretarhabdus*. The numerous species of *Cretarhabdus* do not have great biostratigraphical potential in the Neocomian, and most

were lumped together in the Hauterivian-Barremian of the Speeton section; however all the species were recorded separately in the other sections.

Cretarhabdus angustiforatus (Black, 1971) Bukry, 1973 emend. Bralower *et al.*, 1988

Plate 15, Fig. 2 (EM);
Plate 16, Fig. 4 (LM).

Remarks - Following the emendation of Bralower *et al.* (1988), only forms with a relatively wide central area (>1/3 the minimum diameter of the distal shield) were included in this species. Black (1971) described two very similar forms, *Retecapsa brightoni* and *Retecapsa neocomiana*, which were subsequently utilised by Roth (1978), but these are considered synonymous with *C.angustiforatus*.

Cretarhabdus conicus Bramlette & Martini, 1964

Plate 15, Figs. 7-9 (EM);
Plate 16, Fig. 7 (LM).

Remarks - There is considerable variation within the forms generally assigned to *C.conicus* and these could be subdivided on the LM into a number of categories, based on the development and symmetry of the central cross. Black (1971) described and named a number of such forms using the EM, but light microscopists have so far ignored these species.

Cretarhabdus inequalis Crux, 1987

Plate 15, Fig. 11 (EM);
Plate 16, Fig. 6 (LM).

Remarks - This small form is a rare element of Late Hauterivian to Albian nannofloras. It is only conspicuous in the basal Barremian of the studied sections, shortly above the last occurrence of the light-microscopically similar *Clepsilithus maculosus*. These two taxa are similarly sized and exhibit similar birefringence patterns; the birefringent central bars of *C.inequalis* are, however, fewer in number and much less regularly spaced than those of *C.maculosus*, and the two forms appear very different in phase contrast.

Cretarhabdus madingleyensis (Black, 1968) Crux, 1989

Plate 15, Figs. 5 & 6 (EM).
Plate 16, Fig. 8 (LM).

Remarks - Black (1968) originally described this species from the Oxfordian, but his Jurassic forms have 20 bars in their central grille and are probably indistinguishable from *"Polypodorhabdus" escaigii* Noël, 1965. He subsequently (1971, 1972) described the species in considerably more detail from the Lower Cretaceous; all of his Cretaceous specimens had four bars in each quadrant (= sixteen bars in the grille), and the Hauterivian-Barremian forms were generally larger than older or younger specimens. These observations agree with the present study, in which the concept of *C.madingleyensis* was restricted to large forms (>7μm long) with a relatively wide central area and clear, lath-formed grille. Such forms were only recorded in the Hauterivian-Barremian (with the exception of an isolated occurrence in the Valanginian). Sissingh (1977) probably had a similar concept of *"Cretarhabdus loriei"*, whose first occurrence he used to define the base of his Early Hauterivian *C.loriei* Zone. In this study, smaller, more compact forms with a similar number of shorter bars enclosing rather less slit-like openings were assigned to *C.surirellus*. Crux (1989) recorded *C.madingleyensis* down to the Upper Ryazanian of Speeton, but included small forms and possibly even *C.surirellus* (*sensu stricto*) in his concept. Thus, it could be worth investigating the range and morphometric variation of this species in more detail. This species has open slits between the parallel bars of its central grille, rather than rows of perforations as in *Cretarhabdus striatus*.

Cretarhabdus octofenestratus Bralower in Bralower *et al.*, 1988

Plate 15, Fig. 1 (EM);
Plate 16, Fig. 3 (LM).

Remarks - Differentiated from *C.angustiforatus* by its relatively narrow central area (<1/3 the minimum diameter of the distal shield).

Cretarhabdus radiatus (Worsley, 1971) comb. nov.

Plate 15, Figs. 10 & 12 (EM);
Plate 16, Fig. 5 (LM).

1971 *Rucinolithus radiatus* Worsley, p.1311, pl.1, figs.51-52 (LM).
1988 *Retecapsa radiata* (Worsley, 1971) Applegate & Bergen, p.316, pl.12, figs.5-6 (EM).

Remarks - Applegate & Bergen (1988) demonstrated that *Rucinolithus radiatus* is the radiating distal calyx of a spine-bearing cretarhabdacean similar to *C.angustiforatus*. Isolated calyxes are often encountered on the LM, where they appear as weakly birefringent radiating bodies, similar to *Hayesites*. The coccolith itself is indistinguishable from *C.angustiforatus* in the absence of its distal calyx, but the limited stratigraphical range of this form (Applegate & Bergen, 1988; Bergen, 1994; this study) makes it worth recording the calyxes as a separate species.

Cretarhabdus schizobrachiatus (Gartner, 1968) Bukry, 1969

(syn: *Retecapsa levis* Black, 1971, p.410, pl.33, fig.1 (EM)).

Remarks - Differentiated from *C.angustiforatus* by the very unequal size of its central openings - the four central openings are much larger than the terminal openings.

Cretarhabdus striatus (Stradner, 1963) Black, 1973

1963 *Arkhangelskiella striata* Stradner, p.176, pl.1, fig.1 (sketch).
1966 *Arkhangelskiella striata* Stradner, 1963; Stover, pl.2, figs.3-4 (LM).
non 1968 *Zygolithus striatus* (Stradner, 1963) Stradner *et al.*, p.38, textfig.4 (9) (EM); pl.33, figs.1-2 (EM & LM).
1968 *Cretarhabdus loriei* Gartner, p.21, pl.24, figs.9-10 (LM).
1973 *Cretarhabdus loriei* Gartner, 1968; Thierstein, pl.4, figs.1-2, 4-5 (EM & LM; same specimen).
1973 *Cretarhabdus striatus* (Stradner, 1963) Black, p.53, pl.17, figs.3-6, 10, 11 (EM).
1975 *Allemanites striatus* (Stradner, 1963) Grün & Allemann, p.177 (not illustrated).
1976 *Cretarhabdus striatus* (Stradner, 1963) Black, 1973; Hill, pl.5, figs.7-14 (LM).
1982 *Cretarhabdus striatus* (Stradner, 1963) Black, 1973; Taylor, pl.4.3, figs.15-16 (EM); pl.4.7, fig.19 (LM).

Remarks - Wise (1983) discussed the problems involved in interpreting the holotype of *Arkhangelskiella striata* (Stradner, 1963), but chose to accept the re-illustrated specimens of Stradner *et al.* (1968), which clearly belong to *Crucicribrum*. Nevertheless, the holotypic drawing (and Stover's LMs, which Stradner *et al.* referred to the same species) is considerably larger than *Crucicribrum* and has more numerous central perforations "arranged in lines which meet at oblique angles at the straight central cross" (Stradner, 1963). The holotype also differs from *Crucicribrum* in having a poorly developed short axial cross-bar. All these features leave no doubt that the holotype belonged to the species that Black (1973) featured as *Cretarhabdus striatus*. Black described three subspecies, which seemed to have limited stratigraphical ranges - subsp. *striatus* (Lower Albian),

subsp. *magnus* (Middle Albian), and subsp. *bukryi* (Lower Campanian). The first two subspecies are obviously related, and could be disregarded for LM purposes, but the Campanian form is probably unrelated. See the remarks under *Crucicribrum erraticum* for further clarification of the confusion arising from different interpretations of Stradner's holotype.

Occurrence - This large and conspicuous species is a potentially useful marker. In this study it was only recorded, very consistently, in the Lower Albian of the very incomplete Heslerton Borehole. This fits with the ranges given by Black (1973) and with Thierstein's (1973) first occurrence of *C.loriei* in the Upper Aptian. Similarly, Erba (1988) recorded the first occurrence of *C.striatus* in the Upper Aptian of central Italy. Gartner (1969) described the indistinguishable *C.loriei* from the Cenomanian of the US. Other authors have apparently had much wider concepts of *Cretarhabdus striatus/loriei*, probably including *Cretarhabdus madingleyensis* (see the remarks under this species).

Cretarhabdus surirellus (Deflandre, 1954) Reinhardt, 1970

Plate 15, Fig. 4 (EM).

Remarks - Following Thierstein (1971, p.477) this species is used for all cretarhabdids with a single cycle of greater than eight approximately circular openings around the periphery of the central area (i.e. all forms with more central perforations than *C.angustiforatus*). Thus defined it includes *Cretarhabdus crenulatus* Bramlette & Martini, 1964, which has twelve openings, but such forms are rare. The forms assigned to this species generally have either fourteen or sixteen central openings, and the short axial bar of the central cross is vestigial or missing. Small forms of *C.madingleyensis* are difficult to distinguish from *C.surirellus* on the LM, and were recorded with this species.

Genus *Crucibiscutum* Jakubowski, 1986

Crucibiscutum hayi (Black, 1973) Jakubowski, 1986

Plate 18, Fig. 4 (EM).

1973 *Cruciplacolithus hayi* Black, pl.23, figs.9-10 (EM).
1976 *Cruciplacolithus hayi* Black, 1973; Hill, pl.11, figs.27-28 (LM).
1985 *Sollasites hayi* (Black, 1973) Perch-Nielsen, p.397, fig.6.5.10 (EM).
1989 Large *Crucibiscutum salebrosum* (Black, 1973) Jakubowski, 1986; Crux, pl.8.10, figs.31-32 (LM).

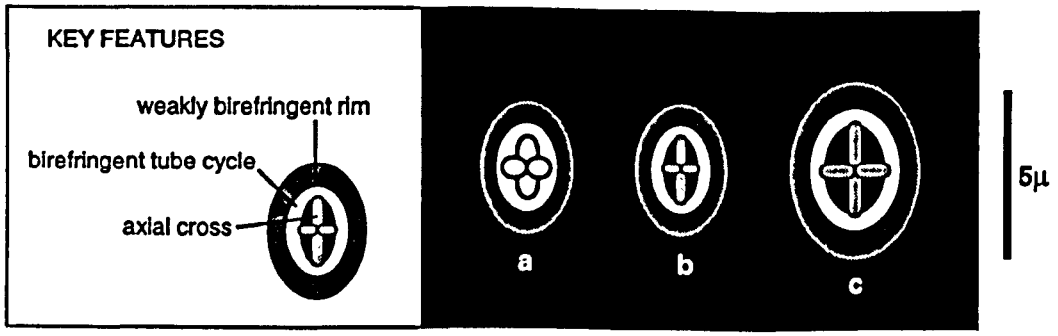
Remarks - Distinguished from *C.salebrosum* and *C.pinnatus* by its larger size, relatively wide central area and relatively narrow rim. The slender-armed axial cross is only weakly birefringent. The overall proportions of this species are more similar to *Sollasites* than to *Biscutum* and, indeed, Perch-Nielsen (1985) included it in the former genus.

Crucibiscutum salebrosum (Black, 1971) Jakubowski, 1986

Plate 9, Fig. 18 (LM).
Plate 18, Figs. 5-7 (EM).

1971 *Cruciplacolithus salebrosus* Black, p.425, pl.30, fig.4 (EM).
1977 *Palaeopontosphaera salebrosa* (Black, 1971) Prins & Sissingh (not illustrated).
1987 *Crucibiscutum salebrosum* (Black, 1971) Jakubowski, 1986; Jakubowski, p.117, pl.2, figs.21-22 (LM).
1989 *Crucibiscutum salebrosum* (Black, 1971) Jakubowski, 1986; Crux, p.185, pl.8.2, fig.8; p.201, pl.8.10, fig.28 (LM).
1991 *Crucibiscutum salebrosum* (Black, 1971) Jakubowski, 1986; Mutterlose, pl.2, fig.1 (EM); pl.11, figs.13-16 (LM).

Remarks - Distinguished from *C.?pinnatus* by its compact central area and birefringent cross. The stubby central cross practically fills the narrow central area, and birefringes with the same intensity as the tube cycle (white). Most previous workers have had a wider species concept, including forms with weakly birefringent crosses here assigned to *C.?pinnatus*. It would seem that Sissingh (1977) had a similarly restricted species concept, since he used the last occurrence of *Palaeopontosphaera salebrosa* to define the top of his Subzone 4A, in the Hauterivian. Black (1971) noted two cycles in the proximal shield of *Cruciplacolithus salebrosus*, but these have not been observed in any published SEMs.



a = *Crucibiscutum salebrosum*
b = *Crucibiscutum ?pinnatus*
c = *Crucibiscutum hayi*

Fig. 2.9 - Schematic differentiation of the species of *Crucibiscutm*, in cross-polarised light.

Crucibiscutum ?pinnatus (Black, 1971) comb. nov.

?1971 *Cruciplacolithus pinnatus* Black, p.397, pl.30, fig.5 (EM).
1982 *Cruciplacolithus salebrosus* Black, 1971; Taylor, p.63, pl.4.2, figs.17-18 (EM).
1983 *Cruciplacolithus salebrosus* Black, 1971; Roth, p.620, pl.30, fig.4 (LM).
1985 *Biscutum salebrosum* (Black, 1971) Perch-Nielsen, p.357, fig.19.24 (EM).
1989 *Crucibiscutum salebrosum* (Black, 1971) Jakubowski, 1986; Crux, p.185, pl.8.2, fig.9 (EM); p.201, pl.8.10, figs.29-30 (LM).

Remarks - Similar to *C.salebrosum*, with which it has been lumped in previous studies, but differs in having a central cross that is only weakly birefringent. The cross does not fill the central area, as in *C.salebrosum*, and leaves four perforations that are clearly visible in cross-polarised light. *C.?pinnatus* was not differentiated from *C.salebrosum* until a late stage in this study, and is included with this species in the range charts (except in Borehole 81/43, where it was recorded separately in the upper part of the section, above the last common occurrence of *C.salebrosum*). This species is always relatively rare, and thus easily overlooked within the range of *C.salebrosum*. Its highest occurrence is in the Lower Barremian; Jakubowski (1987) probably used this last occurrence to define his *C.salebrosum* Zone (NLK 13).

Crucibiscutum* sp. cf. *C.salebrosum

?1983 *Seribiscutum salebrosum* (Black, 1971) Wise, p.545, pl.30, figs.2-3; p.546, pl.31, figs.1-7 (EM).
1987 *Biscutum salebrosum* (Black, 1971) Perch-Nielsen, 1984; Thomsen, p.47, pl.1, figs.21-23 (EM).
1992 *Seribiscutum gaultensis* Mutterlose, p.360, pl.1, fig.4 (EM); pl.6, fig.4? (LM).

Remarks - The forms listed above were recorded from the Aptian of disparate high latitude sites (the Falkland Plateau, North Sea and off N.W. Australia), although the age of the Falkland Plateau specimens (Wise, 1983) remains uncertain. Thomsen (1987) and Mutterlose (1992) recorded the first occurrence of these forms in the Upper Aptian of their sections. Mutterlose (1991) recorded an increase in the abundance of *"Crucibiscutum salebrosum"* (for which he had a broad concept) in the Upper Aptian of Germany. In the present study, such forms, closely mimicking *C.salebrosum*, were recorded abundantly in the Upper Aptian (*nutfieldiensis* ammonite Zone) of Germany and England (in the Fuller's Earth). A certain component of the German forms are almost certainly reworked *C.salebrosum*, since *T.septentrionalis* and *E.striatus* were also recorded in these samples, indicating reworking down to the Upper Hauterivian. However, under close examination (on the LM), most specimens display a subtly

However, under close examination (on the LM), most specimens display a subtly different central area construction to *C.salebrosum*. When rotated under crossed-polars the birefringent central cross displays poorly-developed long axial bars, which may be plate-formed. Dissolution modified forms with only a short axial "bridge" are often observed on the LM, and Thomsen's SEMs display this character.

Genus ***Crucicribrum*** Black, 1973

(new type species: *Arkhangelskiella erratica* Stover, 1966)

Crucicribrum erraticum (Stover, 1966) comb. nov.

non 1966 *Arkhangelskiella striata* Stradner, 1963; Stover, pl.2, figs.3-4 (LM).
1966 *Arkhangelskiella erratica* Stover, p.137, pl.2, fig.10 (LM); pl.8, fig.14 (sketch).
1968 *Zygolithus striatus* (Stradner, 1963) Stradner *et al.*, p.38, textfig.4 (9) (EM); pl.33, figs.1-2 (EM & LM).
1973 *Crucicribrum anglicum* Black, p.62, pl.22, figs.11-15 (EM).
?1973 *Crucicribrum cuniculatum* Black, p.62, pl.22, figs.1-5, 10 (EM).
?1976 *Broinsonia stenostaurion* Hill, p.127-128, pl.3, figs.13-24 (LM); pl.13, figs.12-14 (EM).
1982 *Gartnerago striatum* (Stradner, 1963) Forchheimer, 1972; Taylor, p.69, pl.4.5, figs.12, 15, 16 (EM); p.77, pl.4.8, figs.6-7 (LM).
1983 *Crucicribrum striatum* subsp. *striatum* (Stradner, 1963) Wise, p.507 (not illustrated).
?1983 *Crucicribrum striatum* subsp. *constansii* Wise & Parker in Wise, p.507, pl.23, figs.1-4 (EM); pl.24, figs.1-6 (EM & LM).
1988 *Crucicribrum striatum* ssp. *striatum* (Stradner, 1963) Wise, 1983; Applegate & Bergen, p.320, pl.1, figs.8-12 (EM & LM; same specimen).
?1991 *Crucicribrum anglicum* Black, 1973; Crux, p.215, pl.1, fig.7 (EM); p.217, pl.2, fig.19 (LM).

Remarks - This species was amply described by Stover (1966), but junior synonyms (*Crucicribrum anglicum*) and misassignments (new combinations of *Arkhangelskiella striata* Stradner, 1963) have been propagated throughout the literature for twenty years. Wise (1983) discussed the problems involved in interpreting Stradner's 1963 holotype of *Arkhangelskiella striata*, but chose to accept the re-illustrated specimens of Stradner *et al.* (1968), which clearly belong to *Crucicribrum*. However, as discussed earlier, the holotype of *A.striata* is a cretarhabdid and, in any case, Stover (1966) described *Arkhangelskiella erratica* several years before Stradner *et al.* published their apparently revised (but not amended) description of *Zygolithus striatus*. Thus *C.anglicum* becomes

invalid, and *C.erraticum* must be designated the type species of *Crucicribrum*. *C.cuniculatum* (= *C.anglicum* in Crux, 1991) only differs from *C.erraticum* in having the shorter bar of its central cross offset, and might be regarded as synonymous. Similarly, *C.erraticum* subsp. *constansii* (Wise & Parker in Wise, 1983) cannot be differentiated on the LM and may, in fact, be a diagenetically modified morphotype. Redesignation of *A.erratica* as the type species of *Crucicribrum* frees *A.striata* for use with *Cretarhabdus*.

Genus ***Cyclagelosphaera*** Noël, 1965

Cyclagelosphaera papilla sp. nov.

Plate 13, Figs. 6-10 (EM & LM).

Derivation of name - Latin, *papilla* meaning nipple; referring to the nipple-like appearance of the coccolith in distal view.

Diagnosis - Species of *Cyclagelosphaera* with a monocyclic distal shield and a wide, elevated central plug composed of rudely crystalline elements.

Description (SEM) - Medium to large (5.5-10μm diameter) circular placolith, with a strongly convex, monocylic distal shield composed of approximately 38 dextrally imbricating elements, with laevogyre sutures. The inner edge of this shield, where the precessing sutures are offset to become radial, slopes down to the margin of the central plug. The central plug is approximately 1/3 the diameter of the distal shield, and rises distally above the shield. The plug is imperforate, and composed of coarse, rudely crystalline and irregularly interlocking elements. The proximal surface has not been observed.

Description (LM) - The whole coccolith is highly birefringent (white-yellow), and the wide, imperforate central plug flares markedly on focusing up and down. Occasional side views display a strongly convex distal shield, and wide, distally extending plug.

Differentiation - *C.papilla* is differentiated from all other species of *Cyclagelosphaera* by its wide, rudely crystalline central plug, and its monocyclic distal shield. It is easily differentiated from *C.margerelii* on the LM by its larger size, and its wide, flaring central plug. *C.argoensis* is similarly proportioned but has a bicyclic distal shield and a narrow central tube cycle, enclosing a central perforation; these species are differentiated on the LM by the presence or absence of a central perforation. *C.brezae* also appears similarly proportioned on the LM, but is less birefringent and lacks the flaring central plug of *C.papilla*. *C.alta*, described from the Danian (Perch-Nielsen, 1979), has a similarly elevated central plug, but strut-like outgrowths extend from this structure onto the distal shield.

Occurrence - Upper Hauterivian to Upper Barremian of the North Sea and Barents Sea; generally rare in sections from the North Sea area (Speeton, Borehole 81/43, Germany),

but this dissolution-resistant species is conspicuous within the impoverished Barremian nannofloras of the Barents Sea.

Remarks - LM observations indicate that this species increased in size with time - early forms (Late Hauterivian-Early Barremian) are mainly 5.5µm-7µm in diameter while later forms are >8µm in diameter. The small and large forms were recorded separately.

Holotype - Plate 13, Fig. 6 (EM).

Isotypes - Plate 13, Figs. 7 & 8 (EM).

Type locality & level - Borehole 81/43 (southern North Sea), 17.00m (equivalent to the *variabilis* ammonite Zone; = basal Barremian?).

Genus *Diloma* Wind & Cepek, 1979 emend.

(type species: *Arkhangelskiella primitiva* Worsley, 1971)

Emended Diagnosis - Elliptical murolith with a tricyclic rim composed of inner and outer wall cycles and a proximal plate. The outer wall cycle and proximal plate are only weakly birefringent, while the blocky inner wall cycle is brightly birefringent. A central cross, of variable orientation, arises from the proximal plate. The proximal plate may be detached from the inner wall to form arcuate struts, which may be joined to the inner wall by short, radially arranged bars.

Differentiation - *Diloma* differs from most other muroliths (e.g. the Chiastozygaceae) in having a tricyclic rim (with the addition of an inner, proximal plate to the basic, bicyclic wall construction). It differs from *Eiffellithus* in the relative development of its inner wall cycle (see Remarks under the Eiffellithaceae, and Fig. 2.5). This is the only murolith genus known to exhibit a tricyclic rim extinction pattern.

Remarks - Wind & Cepek (1979, p.228) designated *A.primitiva* as the type species of this genus, but gave a description that allowed inclusion of *Diloma placinum* Wind & Cepek, 1979. *Diloma placinum* (which has not been observed in this study) seems unrelated to *Diloma primitiva*, and should be assigned to another (probably new) genus. *Diloma*, as redefined, seems most closely related to *Eiffellithus*, and is certainly not an arkhangelskiellacean (as suggested by Perch-Nielsen, 1985).

Diloma galiciense Bergen, 1994

Plate 1, Figs. 13-15 (EM);
Plate 2, Fig. 14 (LM).

Remarks - This large (7-9µm long) and distinctive form is assigned to *Diloma* based on the tricyclic appearance of its rim (weakly birefringent outer wall, strongly birefringent inner wall, and weakly birefringent proximal plate). The proximal plate is always

appressed to the inner wall cycle, and is not detached as commonly observed in *Diloma primitiva*. The spine-bearing central cross is oriented in a position intermediate between diagonal and axial.

Occurrence - Lower Hauterivian to Lower Barremian of Speeton and Borehole 81/43. This species is very sporadic in its occurrence (environmentally sensitive?) but is common in a short interval of the Lower Barremian (?) *variabilis* ammonite Zone of both these sections; this brief influx event provides a useful regional tie-point. It has previously been recorded from both Atlantic margins, and S.E. France (Bergen, 1994).

Diloma primitiva (Worsley, 1971) Wind & Cepek, 1979

?Plate 1, Fig. 12 (EM);
Plate 2, Figs. 12-13 (LM).

1971 *Arkhangelskiella primitiva* Worsley, p.1306, pl.1, figs.1-3 (LM).
?1979 *Diloma primitiva* (Worsley, 1971) Wind & Cepek, pl.8, figs.2-3 (LM).
1987 *Diloma placinum* Wind & Cepek, 1979; Covington & Wise, pl.2, figs.1-3 (LM).
?1988 *Diloma primitiva* (Worsley, 1971) Wind & Cepek, 1979; Applegate & Bergen, pl.19, figs.1, 3, 4 (LM & EM; same specimen).
1994 *Diloma* sp.A; Bergen, p.61, pl.1, fig.12 (LM).

Remarks - Prior to Bergen (1994), this species had not been recorded from the North Sea area. However, it was recorded fairly commonly in this study, along with several similar and undescribed forms. Thus, for differential purposes, a description of this species is warranted.

Description (LM) - Medium-sized (about 7μm long) elliptical form with a relatively delicate rim that appears to consist of three narrow cycles: the inner and outer cycles are weakly birefringent (grey) while the middle cycle is brightly birefringent (white). The three cycles may be closely appressed, but the innermost cycle (proximal plate) is commonly detached from the remainder of the rim to form arcuate struts. Only very occasionally could vestiges of the radial bars illustrated by Wind & Cepek (1979) and Applegate & Bergen (1988) be discerned; this may be due to differential preservation, or the forms illustrated by these authors may belong to a different species. The spine-bearing central cross is oriented axially or, occasionally, slightly rotated from the axes of the coccolith. The cross-bars are relatively slender, parallel-sided and generally appear simple, but may appear split along their length in some orientations.

Occurrence - 'Mid' Valanginian to Lower Barremian of the North Sea area; quite sporadic through most of this range, but fairly common in the Lower Hauterivian and Lower Barremian. Applegate & Bergen (1988) recorded *D.primitiva* rarely up to the

Lower Aptian of the Galicia Margin but may have included *Diloma?* sp.1 and *Diloma?* sp.2 in their concept of the species.

Diloma? sp.1

Description (LM only) - Medium-sized (6-7μm long) elliptical form with a relatively narrow, bicyclic rim (narrow, weakly birefringent outer cycle and wider inner birefringent cycle), delicate axial cross, and consequently large central openings. No inner, proximal plate is visible on the LM. The bars of the cross are parallel-sided, and do not appear striate in cross-polarised light.
Occurrence - Rare in the Lower Barremian of Speeton; an isolated record from the Upper Hauterivian of Borehole 81/43 may have been a damaged *Diloma primitiva.*
Remarks - This form is similarly proportioned to *Diloma primitiva*, from which it differs in lacking an inner, faintly birefringent proximal plate; it is almost certainly related to this species, but is only tentatively assigned to the genus due to its lack of the diagnostic tricyclic rim structure.

Diloma? sp.2

1991 *Diloma placinum* Wind & Cepek, 1979; Bralower, fig.6, 11-12 (LM).

Description (LM only) - Medium-sized form (about 6μm long), similar to sp.1 (in lacking an LM visible proximal plate), but more narrowly-elliptical and rather less delicate. The short axial bar of the cross is generally offset slightly, and the cross bears a clear spine.
Occurrence - Rare in the Lower Barremian of Speeton. Bralower's illustrated specimen is from the Lower Barremian of Borehole 81/43.
Remarks - It is possible that this may be an early form of *Acaenolithus* (its SEM ultrastructure is unknown), but it does appear different to *Acaenolithus?* sp.1 on the LM (see remarks under that species).

Genus *Eiffellithus* Reinhardt, 1965 emend. Perch-Nielsen, 1968

Remarks - The genus *Eiffellithus* was originally proposed (Reinhardt, 1965) for Late Cretaceous forms with a bicyclic rim and central cross, and included forms subsequently assigned to *Prediscosphaera.* Perch-Nielsen's (1968) amended diagnosis included only those forms with an outer wall of highly inclined elements and a broad inner cycle of almost horizontally arranged, large platy elements. Applegate and Bergen (1988) considered that the rim structure of several Early Cretaceous forms matched this definition (*Eiffellithus striatus* and two new species, *Eiffellithus windii* and *Eiffellithus*

primus). However their material was not sufficiently well-preserved to demonstrate the non-imbricate, plate-formed nature of the broad, inner rim cycle. When viewed on the SEM this birefringent inner cycle is generally obscured by overgrowth or clay (see Plate 3) but well-preserved specimens (Plate 3, Fig. 3) display the diagnostic arrangement of large platy elements. Several biostratigraphically useful species of *Eiffellithus* have not been fully utilised by previous authors due to their inclusion with light-microscopically similar forms of *Tegumentum* - a whole range of species have often been misassigned to *Tegumentum stradneri. Tegumentum* differs from *Eiffellithus* in having its cross attached to a clearly imbricate inner wall cycle, and in having a lath-formed (rather than fibrous) cross. Despite the previous confusion, the various species of *Eiffellithus* and *Tegumentum* are quite easily distinguished on the LM - these are illustrated in Plate 4, and their stratigraphical ranges summarised in Fig. 2.10. Despite the structural similarities, the Neocomian species of *Eiffellithus* are probably unrelated to mid-upper Cretaceous forms (e.g. *E.turriseiffelii*), which arose in the Late Albian.

Eiffellithus striatus (Black, 1971) Applegate & Bergen, 1988

Plate 3, Figs. 1-6 (EM);
Plate 4, Fig. 3 (LM).

1971 *Chiastozygus striatus* Black, p.433, pl.34, fig.7 (EM).
?1981 *Chiastozygus tripes* Kothe, pl.3, figs. 4-5.
1982 *Tegumentum striatum* (Black, 1971) Taylor, 1978; Taylor, pl.4.4, fig.11 (EM).
1987 *Chiastozygus striatus* Black, 1971; Thomsen, pl.3, figs.1-2 (EM).
1988 *Eiffellithus striatus* (Black, 1971) Applegate & Bergen, p.315, pl.9, figs.1-7 (EM & LM).
1989 *Tegumentum striatum* (Black, 1971) Taylor, 1978; Bralower *et al.*, pl.II, 22-25 (EM & LM).
1991 *Tegumentum striatum* (Black, 1971) Taylor, 1978; Bralower, fig.6, 25-26 (LM).
1991 *Tegumentum tripes* (Kothe, 1981) Mutterlose, 1988; Mutterlose, pl.12, figs. 15-19 (LM).
1992 *Tegumentum striatum* (Black, 1971) Taylor, 1978; Mutterlose, pl.6, figs.9-11 (LM).

Remarks - Crux (1989) included *E.striatus*, *E.windii* and *Tegumentum bergeni* (sp. nov.) in his very broad concept of *Tegumentum striatum*, severely limiting the usefulness of this species in his study. *E.striatus* is characteristically large (>6.5μm long), has a relatively wide central opening, and fibrous cross-bars with flaring, bifurcate terminations. Thus defined, this is an extremely useful cosmopolitan marker species.

Range - Late Valanginian to Late Hauterivian; last occurrence datum in the Late Hauterivian (*speetonensis* ammonite Zone) is probably synchronous world-wide.

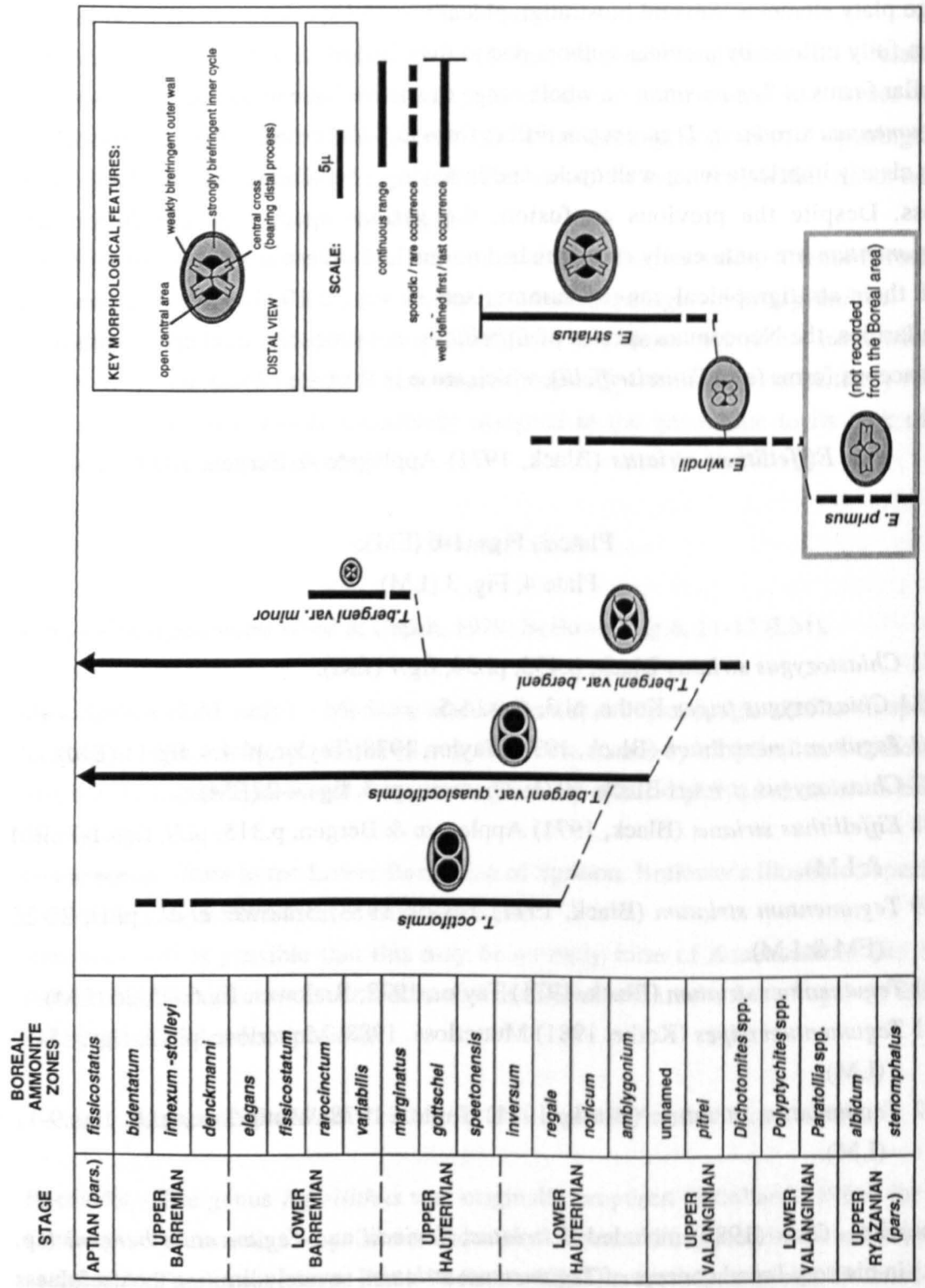


Fig. 2.10 - Key morphological features, stratigraphical ranges and probable evolutionary relationships of Neocomian species of *Eiffellithus* and *Tegumentum*.

Eiffellithus turriseiffelii (Deflandre in Deflandre & Fert, 1954) Reinhardt, 1965

Plate 3, Figs. 8 & 9 (EM);
Plate 4, Fig. 4 (LM).

Remarks - This widely recognised marker species, whose first occurrence has long been used as a Late Albian datum, differs from older, Neocomian forms of *Eiffellithus* in having a hollow (rather than solid) distal process.

Eiffellithus windii Applegate & Bergen, 1988

Plate 3, Fig. 7 (EM);
Plate 4, Figs. 1 & 2 (LM).

Remarks - This species is differentiated from *E.striatus* by its smaller size (<6.5µm long), more compact form (with narrower central openings) and its stubby, non-fibrous, unsplit cross-bars. However, there are forms transitional with *E.striatus*. *E.windii* was grouped with *E.striatus* during counting of the Speeton section; subsequent checking revealed its presence in the *amblygonium* to *regale* Zones (Lower Hauterivian). Bergen (1994) records the highest occurrence of *E.windii* in the lowermost Hauterivian of S.E. France and the western Atlantic but, in this study, *E.windii* was recorded sporadically into the Upper Hauterivian of Borehole 81/43. However, despite this uncertainty, there is a definite change-over in dominance from *windii* types to *striatus* types in the uppermost Valanginian / lowermost Hauterivian. A small (<4µm long), more elongate form, similar to *E.windii* (cf. Bralower *et al.* , 1989, p.207, pl.II, fig.17), lingers on rarely into the Barremian; this could certainly not be confused with *E.striatus*, and may belong to *Tegumentum*.

Eiffellithus **sp.1**

1987 *Eiffellithus?* sp.2 Covington & Wise, p.630, pl.22, figs.7-9 (LM).

Description (LM only) - This medium-sized species has a typical, bicyclic eiffellithid rim and an axial cross. The arms of the cross flare towards their juncture with the rim; this flaring and the fibrous nature of the cross-bars are best observed with the axes of the coccolith oriented at 45° to the polarising directions. This species differs from *Eiffellithus primus*, *Eiffellithus monechiae* and *Eiffellithus eximius* in having a wider central opening and cross-bars that flare towards their juncture with the rim and do not, apparently, overlap the rim. It differs from *Staurolithites? glabra* in having flaring, medianly split cross-bars.

Remarks - Covington & Wise (1987) recorded this species fairly commonly in the Upper Hauterivian (redated here using the last occurrences of *C.cuvillieri* and *S.colligata*) of the western North Atlantic. In this study, it was recorded very rarely in the Hauterivian of Speeton and Borehole 81/43.

Genus *Helenea* Worsley, 1971 emend.

(syn: *Microstaurus* Black, 1971a)

(Type species: *Helenea staurolithina* Worsley, 1971)

Remarks - Grün and Allemann (1975) chose to recognise both *Helenea* and *Microstaurus* as valid genera, but redesignated *Helenea chiastia* Worsley, 1971 as the type species of *Microstaurus*. However, they did not identify *Helenea* in their material, nor did they satisfactorily differentiate the two genera. Following this confusion, most recent authors have disregarded the genus *Helenea*. However, *Helenea* was erected some months before *Microstaurus* and its type species (*H.staurolithina*) appears to be synonymous with the type species of *Microstaurus*, *M.quadratus*. Thus, following a suggestion of Perch-Nielsen (1985, p.385), the genus *Microstaurus* is abandoned in favour of *Helenea*. The emendation proposed below (primarily concerning the orientation of the central cross) allows inclusion of *Watznaueria quadrata* Worsley, 1971 in this genus; this is apt to cause some confusion since *Helenea quadrata* bears the same specific epithet as *Microstaurus quadratus* Black, 1971, which is here regarded as illegal.

Emended Description - Elliptical to circular placoliths, with heavily constructed shields. The larger, distal shield is bicyclic. Both distal shield cycles are only weakly imbricate; the elements of the inner cycle are arranged radially, but those forming the narrower, outer cycle (= the "sickle-shaped elements" of Grün & Allemann, 1975) have clockwise precessing sutures. An open central area is spanned by a cross of variable orientation.

Differentiation - This distal shield construction appears rather watznaueriacean on the LM - the sutures of the rim are tangentially offset towards its outer margin, which is serrate. This rim structure is quite distinct from that of *Cretarhabdus*, *Grantarhabdus*, *Speetonia* and *Cruciellipsis*, whose distal shields are composed wholly of radially arranged elements.

Helenea chiastia Worsley, 1971 emend.

Plate 16, Fig. 1 (LM);
Plate 17, Figs. 4-6 (EM).

1971 *Helenea chiastia* Worsley, p.1310, pl.1, figs.42-44 (LM).

1971 *Microstaurus lindensis* Black, p.405, pl.32, fig.1 (EM).

1972 *Cruciellipsis chiasta* (Worsley, 1971) Thierstein, 1972; Roth & Thierstein, p.437, pl.6, figs.8-13 (EM & LM).

1975 *Microstaurus chiastius* (Worsley, 1971) Grün & Allemann, p.181, pl.5, figs.1-3 (EM).

1976 *Cruciellipsis chiastia* (Worsley, 1971) Thierstein, 1972; Thierstein, pl.IV, figs.28-29 (LM).

1982 *Microstaurus chiastius* (Worsley, 1971) Grün & Allemann, 1975; Taylor, pl.4.3, figs 19-20 (EM); pl.4.7, fig.25 (LM).

1988 *Microstaurus chiastius* (Worsley, 1971) Grün & Allemann, 1975; Applegate & Bergen, pl.27, fig.1 (EM).

1989 *Microstaurus chiastius* (Worsley, 1971) Grün & Allemann, 1975; Crux, pl.8.11, figs.3-4 (LM); pl.8.4, fig.6 (EM).

1989 *Microstaurus chiastius* (Worsley, 1971) Grün & Allemann, 1975 emend. Bralower *et al.*, p.218, pl.V, figs.6-11 (EM & LM).

Remarks - The emendation which Bralower *et al.* (1989, p.218) applied to *M.chiastius* is followed here, in order to differentiate *H.chiastia* from *H.staurolithina* (=*Microstaurus quadratus* in Bralower *et al.*, 1989), with which it is transitional. Thus, the long axis of the central area is less than one half, rather than one third (Worsley, 1971) of the maximum diameter of the distal shield. This species has an axial cross and a prominent four part, blocky spine. Judging from published SEMs, *H.chiastia* seems to vary considerably in form; this species requires further SEM (and specimen transfer) study.

Helenea conus (Worsley, 1971) comb. nov.

1971 *Staurolithites? conus* Worsley, p.1313, pl.2, figs.17-19 (LM).

1979 *Microstaurus conus* (Worsley, 1971) Wind & Cepek, p.230, pl.6, fig.2-3 (LM).

1988 *Microstaurus conus* (Worsley, 1971) Wind & Cepek, 1979; Applegate & Bergen, pl.27, figs.2 & 4-6 (EM & LM).

?1989 *Microstaurus conus* (Worsley, 1971) Wind & Cepek, 1979; Bralower *et al.*, pl.5, figs.13-15 (LM).

Remarks - A large, circular or very broadly elliptical species, with cross-bars that appear bifurcate along their length in both cross-polarised and phase contrast illumination. It is very rare in the study material.

Helenea staurolithina Worsley, 1971 emend.

Plate 16, Fig. 2 (LM).
Plate 17, Fig. 7 (EM).

1971 *Helenea staurolithina* Worsley, p.1310, pl.1, figs.45-47 (LM).
1971 *Microstaurus quadratus* Black, p.404, pl.32, fig.2 (EM).
1979 *Microstaurus chiastius* (Worsley, 1971) Grün & Allemann, 1975; Wind & Cepek, pl.6, fig.1 (EM).
1987 *Microstaurus chiastius* (Worsley, 1971) Grün & Allemann, 1975; Covington & Wise, pl.17, fig.5 (EM).
1989 *Microstaurus quadratus* Black, 1971; Bralower *et al.*, pl.5, figs.1-5 (EM & LM).

Emendation - The long diameter of the central area is greater than or equal to half the maximum diameter of the distal shield. Thus amended, Worsley's description matches that of the now defunct *Microstaurus quadratus* Black, 1971.
Remarks - The flared ends of the axial cross, which are characteristic of *H.staurolithina*, are not always seen on the LM, so this species is more reliably differentiated from *H.chiastia* using the relative size of its central area, as suggested by Bralower *et al.*, 1989. Care must be taken when estimating the relative length of the central area (= cross) and the distal shield, since these depend on the exact plane of focus. This species has a much less prominent spine than *H.chiastia.*

Helenea quadrata (Worsley, 1971) comb. nov.

Plate 17, Fig. 3 (EM).

1971 *Watznaueria quadrata* Worsley, p.1315, pl.2, figs.20-22 (LM).
1994 *Grantarhabdus quadratus* (Worsley, 1971) Bergen, p.61, pl.1, fig.10 (LM).

Remarks - This species has a diagonally oriented central cross; otherwise, its rim appears similar to the other species of *Helenea.* This form has been overlooked by most recent workers, and no published SEMs exist. Bergen (1994) records the highest occurrence of this form in the Upper Hauterivian *ligatus* ammonite Zone of S.E. France. This species was not recognised until a late stage in this investigation, but prior to logging Borehole 81/43. The Hauterivian part of the Speeton section was subsequently re-checked for the species. My highest recorded occurrences of *H.quadrata* are in the middle Hauterivian (uppermost *inversum* ammonite Zone), but it becomes rare towards the top of this range.

Genus *Laguncula* Black, 1971b

Laguncula boletiformis (Black, 1972) comb. nov.

1972 *Parhabdolithus boletiformis* Black, p.29-30, pl.3, figs.3-4; pl.4, figs.1-3 (EM).
1991 *Braloweria boletiformis* (Black, 1972) Crux, p.216, pl.1, figs.8-11 (EM); pl.2, figs.13-18 (LM).

Remarks - *P.boletiformis* and *Laguncula dorotheae* Black, 1971b (the generotype of *Laguncula*) have identically constructed hollow spines, composed of distally imbricating rhombohedral crystals, although the spine is very much more inflated in *L.dorotheae* (compare the EMs of Black, 1972, pl.4 with those of Black, 1971b, pl.2; and compare the LMs of Crux, 1991, pl.2 (fig.17) with those of Wise & Wind, 1977, pl.73, and Wind & Cepek, 1979, pl.11). The "everted flange" (Black, 1971b) at the proximal end of *L.dorotheae* is almost certainly homologous with the murolith rim of *L.boletiformis*. Thus, there is no need for a separate, monospecific genus for this species. *Parhabdolithus judithae* Black, 1972, from the Upper Albian, is very likely the basal rim of *L.dorotheae*. See remarks under *Neoparhabdolithus stubbingsii*.
Occurrence - Black (1972) and Crux (1991) recorded the highest occurrence of this distinctive species in the Middle Albian of southern England; Jeremiah (*in press*) utilises this event to define a zonal boundary. In this study, *L.boletiformis* was recorded in the Lower-Middle Albian of the Heslerton Borehole. It has so far only been recorded from England and the North Sea.

Genus *Manivitella* Thierstein, 1971

Remarks - Recent authors have tended to lump all moderately large, elliptical placoliths with a wide, open central area into *Manivitella pemmatoidea*, and most have included several species of *Tubodiscus* in this category. These two genera are closely related, but quite distinctive (see remarks under the Tubodiscaceae). On the SEM, *Manivitella* differs from *Tubodiscus* in having a short proximal collar, that is inclined inwards (rather than extending vertically) and is thus visible from the distal side (Plate 13, Figs. 11 & 12). Black (1973) recognised several species of *Manivitella*, distinguishing *M.pemmatoidea* from *M.gronosa* on both EM and LM by the cycle of knobs on its distal shield. He recorded the oldest confirmed record of *M.pemmatoidea* in the Albian, noting that he had previously (1971) misidentified *Apertapetra pemmatoidea* in the Hauterivian-Barremian of the Speeton Clay. Black did not, however, refer these records to *M.gronosa*, so it seems that he may have misidentified a species of *Tubodiscus* in 1971. In the present study, forms of *Manivitella* with and without a cycle of birefringent knobs were noted on the LM, but these were not recorded separately. No specimens bearing knobs were ever seen during fairly intensive SEM studies of Neocomian material, so it may be that all the

Neocomian records belong to *M.gronosa.* However, it is possible that the knobs are a preservational artefact.

Genus *Micrantholithus* Deflandre in Deflandre & Fert, 1954

Remarks - The various species of *Micrantholithus* are quite well-defined, and not discussed in detail here. Complete pentaliths are relatively rare, since these have generally disaggregated into their constituent segments. During counting the number of individual segments was recorded and divided by five. Thus the abundance figures reflect numbers of entire pentaliths; where it is abundant *Micrantholithus* accounts for a disproportionately large volume of the sediment.

Micrantholithus obtusus Stradner, 1963

Plate 25, Figs 10 & 11 (EM);
Plate 26, Fig. 5 (LM).

Remarks - Aberrant forms, with the internal margins of their segments thickened, were recorded in the Upper Aptian of the Skegness Borehole. When complete, these forms appear as delicate, birefringent 5-rayed stars; the remainder of the pentalith is thin and only very weakly birefringent. These forms may belong to *Micrantholithus* sp.1 of Perch-Nielsen (1985, p.359), which she indicated to be restricted to the Upper Aptian (N.B. this form differs from *Micrantholithus* sp.1 below).

Micrantholithus **sp.1**

1987 *Braarudosphaera discula* Bramlette & Riedel, 1954; Covington & Wise, pl.4, fig.4 (LM).

Description - Small (c.4-5μm diameter), circular species of *Micrantholithus*; the outer margin of each segment is convex, giving the complete pentalith a circular outline.
Remarks - The constituent segments of this form have almost always separated (only one entire specimen was recorded) and, due to their small size, low birefringence and similarity to nannoconid plates (which are common at some levels) they are easily overlooked. However, once identified, these segments were observed quite commonly at levels where other, larger, species of *Micrantholithus* were common. This species is similar in shape to *Braarudosphaera discula*, but the latter species is much larger, more strongly constructed (it does not tend to disaggregate) and is not recorded below the Upper Aptian. According to most authors' criteria this species should be placed in *Braarudosphaera*, rather than *Micrantholithus*, but it is felt that in Mesozoic forms, at

least, the fundamental distinction between these genera lies in the method by which their segments are joined, rather than the actual shape of these segments (the pentaliths of *Braarudosphaera* are much more ruggedly constructed, and do not tend to break up).
Occurrence - Lower Hauterivian to Lower Barremian of Borehole 81/43; this species was not identified until a late stage in this study, and is not recorded in the other sections. Applegate & Bergen (1988) probably included this species in their concept of *B.discula*, which they recorded down to the Upper Valanginian of the Galicia Margin. Thierstein (1971) included such forms "intermediate...between *Micrantholithus hoschulzii* and typical *Braarudosphaera bigelowii*" in his concept of *B.bigelowii*, thus giving a composite range of Lower Berriasian to Recent.

Genus *Nannoconus* Kamptner, 1931

Remarks - Nannoconids are of unknown biological affinity so the terms proximal and distal, which imply positions on a living cell, cannot strictly be applied. Nevertheless, the radiating rosette groupings described by Trejo (1961) indicate a life association comparable with coccoliths. In these groups of *N.steinmannii* the wider "basal" ends of the conical nannoconids are located distally to the centre of the rosette; not proximally, as figured by Deres and Achéritéguy (1980, p.7) in a hypothetical reconstruction of a *Nannoconus* cell. Thus, it is proposed that the term "basal" be dropped and replaced by "antapical", indicating the opposite end to the apex (and a probable distal position). In any case, these terms can only be applied to conical or asymmetrically developed nannoconids; parallel-sided forms cannot be oriented in this way. In the following descriptions the more prominently flared end of a nannoconid is assumed to be its antapical end.

Due to the limitations of their basic architecture (= a cone/pillar constructed from spirally arranged rows of plates) nannoconids are especially prone to homeomorphy, and thus to misidentification. Nannoconids are generally much more abundant at Tethyan sites and, due to the relatively poor preservation of the coccoliths in these sections, the nannoconids have tended to be over-split. Thus a number of described species are probably conspecific. Nannoconids conforming with the various types described from Tethys (*N.steinmannii*, *N.kamptneri*, *N.globulus*, etc.) are relatively rare in the studied material, and are not discussed any further in this section. The only abundant nannoconids are apparently endemic, Boreal forms, and these are concentrated in two main intervals - the basal Valanginian (*N.oviformis*) and the mid-Barremian (*N.abundans* and allies). Only two endemic Boreal species have previously been described from the Barremian - *N.abundans* and *N.borealis* - but a number of other morphotypes were observed here. The Barremian nannoconids are very different to contemporaneous Tethyan forms, but are so variable in morphology, with many gradational types, that there is a distinct danger

of over-splitting. Only two of these new morphotypes are given specific status (*N.inornatus* sp. nov. and *N.pseudoseptentrionalis* sp. nov.). These have different ranges to other, previously described species, and are found in monospecific nannoconid associations; thus they probably represent biologically distinct species. Other distinctive, but apparently intergradational morphotypes, are described as varieties of pre-existing species. A number of other fairly distinctive, but uncommon types are recorded as "sp".

The sudden proliferation and diversification of endemic forms of *Nannoconus* during the Early Barremian is linked to changing palaeogeographical and palaeoclimatic conditions. This diversification began when a short, flangeless nannoconid, of probable Tethyan origin (*N.inornatus*), became isolated in an unusually favourable North Sea basin, due to widespread regression at this time. Adaptive radiation gave rise to many bizarre forms, never encountered in Tethys, and a number of homeomorphs of Tethyan species. The development of an antapical flange, giving *N.abundans*, was a highly successful innovation, carried to its extreme development by *N.borealis* (in which the plates of the flange have thickened and rotated). These are the only two flanged species generally recognised, but gradations between these two end members are observed. A further innovation was the development of an apical flange, giving biflanged forms reminiscent of the much older *N.concavus* (Boreal) and *N.quadratus* (Tethyan). The biflanged forms also show great variation in size, height/width ratio, and in the relative development of their apical/antapical flanges. The flangeless ancestral species survived throughout the Early Barremian, showing considerable variation in height/width ratio and in the relative width of the axial canal, and probably gave rise to homeomorphs of the Tethyan species *N.elongatus.* All of these forms are provisionally assigned to the "*N.abundans* group".

Nannoconus abundans Stradner & Grün, 1973

Plate 22, Figs. 8-11 (EM);
Plate 23, Figs. 5-8 (LM);
Plate 24, Figs. 1 & 2 (EM).

Remarks - Only forms with a clear antapical flange were included in *N.abundans*; some previous workers have included flangeless forms, here assigned to *N.inornatus.* These forms are easily distinguished in side view, but differentiation of end views is rather more difficult (early, narrow-flanged forms of *N.abundans* appear similar to *N.inornatus*). *N.abundans* often has a small apical flange, giving the test a concave profile, but forms with equally well-developed apical and antapical flanges were recorded separately, as *Nannoconus* sp. (biflanged). *N.abundans* shows considerable variation in size, and in the relative width of its main, antapical flange. Two varieties were recorded - var.1 has a relatively narrow flange (< twice the diameter of the test) and var.2 has a wide

flange (> twice the diameter of the test). There does not, however, seem to be a significant difference in the ranges of these varieties. The flanges of the wider-flanged variety are often very asymmetrically developed. There is also considerable variation in the development of vertical ribbing: some forms are highly ribbed, so that the margin of the test appears scalloped in end view, while others are smooth-sided and appear perfectly circular in end view.

Occurrence - Lower Barremian (*rarocinctum* Zone) to lowest Aptian (?) of the North Sea area, and the Barents Sea. Applegate and Bergen (1988) recorded *N.abundans* from the Barremian of the eastern Atlantic but did not illustrate the species, so their species concept may have been different.

Nannoconus borealis Perch-Nielsen, 1979

Remarks - This species shows considerable, probably ontogenetically-related, variation in form - a number of similar morphotypes seem to have concurrent ranges, and likely represent the growth stages of a single species. *N.borealis* has been used as a zonal marker (Jakubowski, 1987), so it is important that the species be unambiguously defined. I have thus recognised two varieties: var.A (= incompletely formed) and var.B (= fully-formed, "classic" *N.borealis*). Recognition is further complicated by fragmentation of individuals - these fragments may resemble other, Tethyan nannoconids.

Nannoconus borealis var.A

Plate 22, Fig. 7 (EM);
Plate 23, Figs. 9 & 10 (LM);
Plate 24, Figs. 3 & 4 (EM).

1987 *Nannoconus* spp. Thomsen, pl.10, figs.4-5 (EM); pl.11, fig.25 (LM).

Description (LM & EM) - Transitional in form between *N.abundans* and *N.borealis*. The pillar-like part of the test is very much taller than in *N.abundans*, but similarly constructed from thin, shallowly spiralling plates. The well-developed antapical flange is approximately horizontal or slightly inclined antapically, and its constituent plates are thickened. There may be a rudimentary apical flange. The test is 10-20μm high.

Differentiation - This form is much taller than *N.abundans* (its height is greater than twice the diameter of the main part of the test), and lacks the very thickened, bulbous antapical end of *N.borealis* var. B.

Occurrence - 'Mid' to Upper Barremian of the North Sea area.

Nannoconus borealis var.B

Plate 22, Figs. 1-5 (EM);
Plate 23, Figs. 11 & 12 (LM).

Description (LM & EM) - This variety includes typical, fully-formed specimens of *N.borealis* with an expanded, bulbous antapical end composed of coarse plates. The remainder of the test is constructed similarly to *N.abundans*, but is much taller and occasionally slightly curved. This form is often broken - the isolated swollen antapical part is quite distinctive (Plate 23, Fig. 12), but the elongate part of the test might be mistaken for *N.elongatus* or *N.bermudezi* (Plate 22, Fig. 5). The overall size of the test is quite variable (10-25µm long). As with *N.abundans*, the elongate part of the test may be vertically ribbed.
Occurrence - 'Mid' to Upper Barremian of the North Sea area.

Nannoconus inornatus sp. nov.

Plate 22, Figs. 12-16 (EM).
Plate 23, Figs. 1-4 (LM).

1982 *Nannoconus abundans* Stradner & Grün, 1973; Taylor, pl.4.6, fig.19 (EM).
1987 *Nannoconus abundans* Stradner & Grün, 1973; Thomsen, pl.6, fig.10-11 (EM).

Derivation of name - Latin, *inornatus* meaning unadorned; referring to the simple, unflanged form of this species.
Diagnosis - A short, biconcave, pillar-like nannoconid composed of thin plates arranged in a very low-angled spiral, with a narrow axial canal.
Description (LM & EM) - The sides of the test are convex, and the ends unflared, slightly concave and identical; thus apical/antapical ends cannot be distinguished. The height of the test is generally less than its diameter, often considerably less. The axial canal is very much narrower than the wall of the test. The outer surface of the wall is smooth, giving a circular profile in end view. The thin plates composing the wall are arranged in a very low-angled spiral. This is a medium-sized form, with a fairly consistent diameter of 5-7µm.
Differentiation - This species differs from *N.abundans* in lacking an antapical flange, from *N.circularis*, *N.globulus* and *N.inconspicuous* in having a narrower central canal, and from *N.ligius* in its non-petalloid profile.
Occurrence - Hauterivian-Barremian of the North Sea area; rare through the lower part of this range, but became common/abundant in the Early Barremian, just prior to the inception of *N.abundans*.

Remarks - This is the obvious ancestor of *N.abundans*, but it is important to separate these forms since inclusion of this form in *N.abundans* gives an anomalously early first occurrence for that important marker species (e.g. Taylor, 1982; Thomsen, 1987). Two varieties of this species were recorded: a larger, highly birefringent variety (var.1), and a smaller, shorter variety (var.2) yielding only white birefringence in end view. This species developed vertical ribs in the upper *fissicostatum* Zone, giving it a regularly scalloped margin in end view; these ribbed forms probably gave rise to *N.pseudoseptentrionalis* in the *elegans* Zone.

Holotype - Plate 22, Fig. 12.

Isotype - Plate 22, Fig. 16.

Type locality & level - Borehole 81/43 (southern North Sea); 14.70m (Lower Barremian).

Nannoconus pseudoseptentrionalis sp. nov.

Plate 23, Figs. 14-15 (LM).

?1987 *Nannoconus quadriangulus* subsp. quadriangulus Deflandre & Deflandre-Rigaud, 1967; Thomsen, pl.6, figs.6, 7, 9 (EM).

1989 *Tegulalithus septentrionalis* (Stradner, 1963) Crux, 1986; Crux, pl.8.9, figs.5 & 6 (EM).

Derivation of name - After the Greek *pseudes* (= false), i.e. false-*septentrionalis*.

Diagnosis - A short, flangeless nannoconid with a very narrow axial canal, and an irregular, ragged margin, as seen in end view.

Description (LM & EM) - This species is so short that it has only been seen in end view. The thin, shallowly spiralling plates, composing the test, overlap irregularly to give a ragged margin. This form lacks regularly spaced vertical ribs, and thus its margin is not regularly scalloped. The axial canal is much narrower than the width of the wall. The strongly birefringent test is 5-7μm in diameter.

Differentiation - This form is differentiated from other similar nannoconids by its irregular, ragged margin; this renders it similar to *Tegulalithus septentrionalis* in cross-polarised light, and it has been misidentified as such in several previous studies. These optically similar species are readily differentiated in phase contrast (in which *T.septentrionalis* displays regularly-spaced wall elements), and in side view (*T.septentrionalis* is commonly encountered in highly distinctive side view). In end view *N.pseudoseptentrionalis* lacks the weakly birefringent flanges often (but not always) seen on *T.septentrionalis*.

Holotype - Crux, 1989, p.199, pl.8.9, fig.5 (EM).

Isotype - Crux, 1989, p.199, pl.8.9, fig.6 (EM).

Type locality & level - Gott Pit (Germany), Bed 109 (mid-Barremian; *Aulacoteuthis* belemnite Zone).
Occurrence - 'Mid' Barremian of the North Sea area. This species is common in the Lower Cement Beds of Speeton (*elegans* ammonite Zone) and at a corresponding level in Germany; it is associated with common/abundant *Zeugrhabdotus scutula* at both localities.

Nannoconus sp. (short, biflanged)

1987 *Nannoconus* spp. Thomsen, p.65, pl.10, fig.8 (EM).

Description - Very similar to *N.abundans*, but differs in possessing equally well-developed apical and antapical flanges. Similar, biflanged forms have been described from the Tithonian-Valanginian of Tethys (*N.quadratus* Nöel, 1958) and the Upper Ryazanian to basal Valanginian of the North Sea (*N.concavus* Perch-Nielsen, 1988). *N.quadratus* has a much wider axial canal than the forms observed in this study, and *N.concavus* has more rudimentary flanges; both these species are, in any case, separated from these Barremian forms by a wide stratigraphical gap.
Occurrence - 'Mid' Barremian of the North Sea area, first appearing shortly after the closely-related *N.abundans*.

Nannoconus sp. (tall, biflanged)

1987 *Nannoconus* spp. Thomsen, p.65, pl.10, fig.7 (EM).

Description - This form has equally developed apical and antapical flanges, and is taller than its maximum width (measured across a terminal flange).
Occurrence - Rare in the mid-Barremian of the North Sea area.
Remarks - These may be aberrant specimens of *N.borealis*.

Genus *Neoparhabdolithus* gen. nov.

(type species: *Parhabdolithus stubbingsii* Black, 1971)

Diagnosis - Elliptical murolith with a high, distally flaring wall composed of non-imbricating elements, a prominent distal process whose broad, granular base completely fills the central area, and a basal grid composed of bars aligned parallel with the short axis of the coccolith.
Differentiation - *Parhabdolithus* Deflandre, 1952 is applied to similar, spine-bearing, conical muroliths from the Lower Jurassic; *Neoparhabdolithus* differs from these Liassic

forms in possessing a proximal grid (although this is not always preserved), and in the morphology of the distal process. The process of *Neoparhabdolithus* is thin-walled and hollow, with a granular texture; Liassic species of *Parhabdolithus* have much more solidly constructed spines. In any case there is a huge disparity in the ranges of these forms (Lower Jurassic to Valanginian), and any direct genetic relationship is unlikely. *Parhabdolithus* is considered inappropriate for Cretaceous forms, and should not be used in the much broader sense of many authors, who include various Cretaceous rhagodiscids and zeugrhabdotids in this genus. *Braloweria* Crux, 1991 (which is here regarded as a junior synonym of *Laguncula*) is similarly constructed, but has a much lower wall of imbricate elements.

Remarks - Due to their relatively narrow, elliptical bases and tall spines these species are invariably encountered in side view, on both LM and SEM. Thus previous authors, not confident in the differentiation of side views, have overlooked them. Nevertheless, the several species are very distinctive on the LM, and occasionally common.

Neoparhabdolithus stubbingsii (Black, 1971) comb. nov., emend.

Plate 7, Figs. 1-7 (EM & LM).

1971 *Parhabdolithus stubbingsii* Black, p.394, pl.33, figs.10-11 (EM).

Emended Description - Species of *Neoparhabdolithus* with a long, tapering spine that flares slightly at its distal extremity to form a small calyx.

Remarks - Black's (1971) holotype has a long, tapering spine but its distal end is missing, and he did he not describe the spine. Applegate & Bergen (1988) illustrated a similar form (*Parhabdolithus* sp.; p.342, pl.23, figs.10-12) from the Upper Albian or Lower Cenomanian of offshore Spain, but the walls of its spine are birefringent, rather like *Laguncula boletiformis.*

Occurrence - Lower Hauterivian to Lower Barremian of Speeton and Borehole 81/43; rare through most of this range, but quite common in the Upper Hauterivian of Borehole 81/43.

Neoparhabdolithus sp.1

Plate 7, Figs. 8-9 (EM).

1987 *Chiastozygus cepekii* Crux, pl.1, fig.18 (LM); *non* figs.19-20.

1989 *Chiastozygus cepekii* Crux, 1987; Crux, pl.8.12, figs.10, 13, 14 (LM); *non* figs.11-12.

Description (LM & EM) - A species of *Neoparhabdolithus* with a relatively short, broadly flaring distal process.

Remarks - Broken specimens of *N.stubbingsii* may have been included with *Neoparhabdolithus* sp.1 during LM logging, but the latter form does seem to be the longer-ranging of the two. These two forms might, however, be conspecific, and require further SEM study.

Occurrence - Lower Valanginian to mid-Barremian (composite range) of the North Sea and Barents Sea; this form was recorded in every section within this age bracket. It is rare through most of this range, but occasionally common.

Genus *Perissocyclus* Black, 1971

Remarks - Podorhabdids of the Jurassic and Late Cretaceous seem to maintain consistent numbers of central perforations, enabling definition of genera such as *Tetrapodorhabdus*, *Hexapodorhabdus*, *Octopodorhabdus*, *Dekapodorhabdus* and *Dodekapodorhabdus*, based on the number of pores. However, Black (1971, p.405) noted "a peculiar freedom" in the central structures of the Early Cretaceous species that he assigned to this genus. Thus, these species, and forms later assigned to *Perissocyclus*, have been rather poorly defined. The smaller forms (*P.fletcheri* and *P.noelae*) cannot be differentiated in cross-polarised light - their pores can only be counted in phase contrast illumination, and only when well-preserved. These small forms have been lumped into *Perissocyclus* sp. (small). The larger forms, however, are quite distinctive - *P.plethotretus* and *P.tayloriae* are potentially useful markers if they are more accurately defined. These forms are more usefully defined using simple LM criteria (size and birefringence of the central bars).

Perissocyclus fletcheri Black, 1971

Remarks - Black (1971) defined this species very loosely, recording 10-16+ central perforations, in one or two concentric rings, within a relatively narrow central area. Crux (1989, p.190) noted that this was, "a distinctive species.....with ten central perforations". Both authors found it to be restricted to the Upper Ryazanian. In the present study, only small forms (about 5µm long) with ten perforations (visible only in phase contrast) in an outer cycle were recorded as *P.fletcheri*. Such forms do appear to be restricted to the Upper Ryazanian, but it remains to be seen whether they can be reliably differentiated from *P.noelae*.

Perissocyclus noelae Black, 1971

Plate 17, Figs. 8 & 9 (EM).

Remarks - Black (1971) defined this species as having a single cycle of 5-9 perforations. In this study, small forms with less than 10 perforations in the outer ring were recorded as *P.noelae* but, since phase contrast illumination was not used routinely, these forms were generally recorded as *Perissocyclus* sp. (small).

Perissocyclus plethotretus (Wind & Cepek, 1979) Crux, 1989 emend.

Plate 6, Figs. 1 & 2 (LM);
Plate 17, Figs. 10-14 (EM).

non 1966 *Zygolithus fenestratus* Stover, p.147, pl.3, fig.21, 22c (LM); pl.4, fig.1 (LM); pl.8, fig.24.

?1971 *Perissocyclus fenestratus* (Stover, 1966) Black, p.406, pl.32, fig.4 (EM).

1979 *Octopodorhabdus plethotretus* Wind & Cepek, p.230, pl.4, figs.1-5 (EM & LM).

1982 *'Dodekapodorhabdus noelii'* Perch-Nielsen, 1968; Taylor, pl.4.1, fig.12, 14 (EM); pl.4.7, fig.5 (LM).

1988 *Octopodorhabdus plethotretus* Wind & Cepek, 1979; Applegate & Bergen, pl.29, figs.3, 4, 7 (EM & LM).

1989 *Perissocyclus plethotretus* (Wind & Cepek, 1979) Crux, p.190, pl.8.11, figs.?25, ?26, 27 (LM).

1991 *Perissocyclus fenestratus* (Stover, 1966) Black, 1971; Bralower, fig.6, 1-2 (LM).

1991 *Dodekapodorhabdus noelii* Perch-Nielsen, 1968; Bralower, fig.6, 3-4. (LM).

?1991 *Dekapodorhabdus typicus* Medd, 1979; Bralower, fig.6, 5-6 (LM).

Emended Description - Large (>7μm long) podorhabdacean with an outer cycle of 12 (very occasionally 10 to 14) large perforations separated by clearly birefringent struts. An additional inner cycle of perforations may be present, but these are not normally visible on the LM. The bars adjoining the central spine may be thickened to form buttresses.

Remarks - Wind and Cepek (1979, p.231) noted that in Hauterivian podorhabdids, "the size of the entire specimen and width of the individual holes is related to the number of holes present.....those with 12 or more holes approach 7μm in greatest dimension". They used size as the principle criterion to differentiate *P.plethotretus* from *P.noelae*, with *P.noelae* 5-7μm long and *P.plethotretus* generally greater than 10μm long. Increased size also results in an increase in birefringence. In the studied sections, large multi-perforate forms with birefringent struts first appear in the mid-Hauterivian. It seems that once a certain size (and number of perforations) was attained a "birefringence threshold" was crossed. Smaller (6-7μm long) forms with an outer cycle of 12 perforations separated by non-birefringent struts (only visible in phase contrast) were recorded as *Perissocyclus "proto-plethotretus"*. The number of perforations in the

marginal cycle of *P.plethotretus* was observed to be remarkably consistent - there are almost invariably 12, and specimens with more or less pores may be aberrant. Only ten perforations are visible in the holotypic LMs of Wind & Cepek (1979), but an SEM of the same specimen shows 12 marginal perforations (these are unequal in size, with the lateral ones being much smaller). The isotype has an outer cycle of 12 equally sized perforations. See the remarks under *Rhagodiscus fenestratus* for clarification of the confusion arising from different interpretations of Stover's *Zygolithus fenestratus.*

Occurrence - This species appears abruptly in the mid-Hauterivian of the studied sections. Taylor (1982) noted the first occurrence of *'Dodekapodorhabdus noelii'* in the latest Hauterivian *marginatus* ammonite Zone of Speeton, shortly above the unexposed C4-C5 interval, but *P.plethotretus* occurs consistently throughout this interval in Borehole 81/43 and rarely in the uppermost *inversum* ammonite Zone at Speeton. Mutterlose (1991) recorded *P.plethotretus* very sporadically down to the *discofalcatus* ammonite Zone in Germany; in this study it was recorded fairly consistently down to the considerably older *staffi* Zone in the limited German material. Crux (1989) recorded *P.plethotretus* down to the basal Hauterivian of Speeton and Germany, but included smaller forms with non-birefringent struts. Applegate & Bergen (1988) recorded this species down to the Lower Valanginian of the Galicia margin; the only form they illustrate (from the Upper Hauterivian) has birefringent struts, so it is possible that they too had a wider concept of this species. Wind & Cepek (1979) recorded *O.plethotretus* in the ?Hauterivian of the N.W. African margin. All this evidence indicates a first occurrence in the mid-Hauterivian, in the North Sea area at least. The last occurrence of this species cannot be determined from the limited sections available, and it may be transitional with *Octocyclus magnus* in the Aptian, but it certainly ranges through the Lower Barremian unchanged.

Perissocyclus tayloriae Crux, 1989 emend.

Plate 6, Figs. 4 & 5 (LM).

Emended Description - Large podorhabdacean (generally >10μm long) with multiple cycles of small perforations, separated by birefringent bars. The multiple cycles of perforations are visible in cross-polarised light, but only the outer cycle is well enough defined to be easily counted; this outer cycle contains at least 16 perforations (16, 18, and 20 have been observed). The central spine may be supported by buttresses.

Remarks - Crux's (1989) diagnosis of this species cannot be differentiated from *P.plethotretus*, although this is possibly due to a typing error - "8 to 22 small central perforations" should perhaps have been "18-22". There seems to be a general reduction in the number of perforations with time - the earliest forms recorded in Borehole 81/43 have 20 perforations in the outer cycle, while later forms have only 16.

Occurrence - Quite common in the Upper Hauterivian of Borehole 81/43, in the interval that is unexposed at Speeton, and also recorded from this same interval in Germany. Only rare, smaller, 16-holed forms occur above this interval - these were probably included with *P.plethotretus* in the Speeton section.

Pickelhaube furtiva (Roth, 1983) Applegate *et al.* in Covington & Wise, 1987

Plate 16, Fig. 14 (LM).

Remarks - This species has a very peculiar rim, with a tiny but birefringent distal shield, and an expanded, weakly birefringent proximal shield. It was recorded very rarely in the Lower Hauterivian to Upper Barremian of Speeton and Borehole 81/43. No central structure was ever observed, even in phase contrast. Thus, these specimens may be more akin to *Pickelhaube* sp.1 of Applegate & Bergen (1988), which has an open central area and seems (from their SEMs) to be a distinct species rather than a dissolution product of *P.furtiva.*

Genus ***Podorhabdus*** Noël, 1965 emend. Wind & Wise in Wise & Wind, 1977

Hemipodorhabdus gorkae (Reinhardt, 1969) Grün in Grün & Allemann, 1975

Plate 16, Fig. 15 (LM).

Remarks - There are forms gradational between *H.gorkae* and *Tetrapodorhabdus coptensis* Black, 1971, with minuscule openings in the minor axis, and these species are perhaps best included together for LM purposes.

Genus ***Radiolithus*** Stover, 1966 emend. Varol, 1992

Radiolithus antiquus (Perch-Nielsen, 1979) comb. nov.

Plate 19, Figs. 1, 2, 4, & 5 (EM);
Plate 20, Figs. 1 & 2 (LM).

1979 *Eprolithus antiquus* Perch-Nielsen, p.265, pl.1, figs.4-8 (EM & LM).
1989 *Eprolithus antiquus* Perch-Nielsen, 1979; Crux, pl.8.9, figs.9 & 12 (EM); pl.8.14, figs.13, 18, 23 (LM).
1992 *Eprolithus? antiquus* Perch Nielsen, 1979; Varol, pl.1, figs.19-20; pl.5, fig.16 (LM).

Remarks - Having revised the taxonomy of the Polycyclolithaceae, Varol (1992) only tentatively retained this species (whose SEM ultrastructure was poorly known) in the genus *Eprolithus*. The SEM ultrastructure of this species (Plate 19) shows that it should be reassigned to *Radiolithus*, as redefined by Varol (1992). Both cycles of the wall are constructed from non-imbricating, brick-like elements, while the central diaphragm is composed of dextrally imbricate elements. The two wall cycles are of different height, with the diaphragm amedianly positioned. This form differs from later species of *Radiolithus* in having a perforation through the centre of its diaphragm and is, in any case, separated from later forms by such a wide stratigraphical gap that it is probably unrelated. The number of elements in each cycle of the wall appears to be slightly variable (10-12), but these are invariably rudely formed and difficult to count.

Genus ***Rhabdophidites*** Manivit, 1971 emend. Lambert, 1987

(syn: *Rhabdolekiskus* Hill, 1976)
(?syn: *Pseudolithraphidites* Keupp, 1976)

Remarks - The forms herein assigned to this genus have been subject to considerable taxonomic reshuffling, being variously assigned to *Rhabdolekiskus*, *Rhabdophidites*, *Pseudolithraphidites*, and *Vekshinella*. Only one species (*R.parallelus*) was observed in the present study, but the clearly-related *Vekshinella pseudocarinolithus* is reassigned. These species have an axially aligned cross in their basal disk, hence their previous assignment to *Vekshinella* (=*Staurolithites*), but this resemblance to *Staurolithites* may be only accidental, with the basal cross reflecting the cruciform section of the rod. In any case, these forms are sufficiently distinctive to warrant separate generic status. *Rhabdophidites* was originally applied (Manivit, 1971) to a similar form that tapered at both ends (*R.aquitanicus*). This genus is assigned to the Microrhabdulaceae, based on its close similarity to *Lithraphidites* - this similarity suggests that *Lithraphidites*, which is generally regarded as a nannolith, may be of coccolithophorid origin. *Pseudolithraphidites*, which was described from the Tithonian, lacks any basal disk.

Rhabdophidites parallelus (Wind & Cepek, 1979) Lambert, 1987

Plate 2, Fig. 11 (LM);
Plate 25, Figs. 13 & 14 (EM).

Range - Mid-Valanginian to Aptian/Albian; lowest recorded occurrences in the Mid-Valanginian of Borehole 81/43 (this study) and the *campylotoxum* ammonite Zone of S.E. France (Bergen, 1994).

Rhabdophidites pseudocarinolithus (Applegate & Bergen, 1988) comb. nov.

1988 *Vekshinella pseudocarinolithus* Applegate & Bergen, p.317, pl.16, figs.1-9 (EM & LM; same specimen).

Remarks - This species was not recorded in this study; it is apparently virtually confined to the Valanginian (Applegate & Bergen, 1988).

Genus **Rhagodiscus** Reinhardt, 1967

Rhagodiscus achlyostaurion (Hill, 1976) comb. nov.

Plate 6, Figs. 13, 17 (LM).

1976 *Parhabdolithus achlyostaurion* Hill, p.145-6, pl.9, figs.24-29 (LM).

Remarks - This species has been ascribed to *Rhagodiscus* by several authors (Crux, 1991; Mutterlose, 1991), but has not been formally reassigned. Under crossed-polars its rim appears rather more complicated than in other rhagodiscids, with an additional, narrow, inner cycle, but the most distinctive feature of this species is its prominent circular spine base; this is the most birefringent part of the coccolith. Roth (1983) recorded *P.achlyostaurion* rarely in the Valanginian of the western Atlantic, but these forms were almost certainly attributable to *Rhagodiscus dekaenelii* Bergen, 1994. Erba (1988) used the first occurrence of this form in central Italy to define the base of her Upper Albian *P.achlyostaurion* Zone, but Crux (1991) recorded it down to the base of his Middle Albian English section. This apparent diachroneity may be due to slightly different species concepts.

Rhagodiscus angustus (Stradner, 1963) Reinhardt, 1971

Remarks - Numerous authors have used the first occurrence of this species to mark the base of the Upper Aptian (Manivit, 1971; Thierstein, 1973, 1976; Perch-Nielsen, 1979; Taylor, 1982; Jakubowski, 1987; Erba, 1988) but similar, though smaller forms are common in the lowermost Aptian of the North Sea area (Thomsen, 1987, and this study). Thus, Mutterlose (1991), who did not differentiate the small and large types, recorded *R.angustus* down to the base of the Aptian in Germany. This species is divided into two subspecies to clarify this biostratigraphical ambiguity.

Rhagodiscus angustus subsp. **angustus** (Stradner)

Plate 6, Fig. 16 (LM).

1963 *Rhabdolithus angustus* Stradner, p.178, pl.5, fig.6 (sketch).
1985 *Rhagodiscus angustus* (Stradner, 1963) Reinhardt, 1971; Perch-Nielsen, p.395, fig.63. 10-13, 15-16 (EM & LM).
1987 *Rhagodiscus angustus* (Stradner, 1963) Reinhardt, 1971; Thomsen, pl.16, fig.9.

Description - Elongate (length/width ratio of ≥ 2.5) form, with parallel or slightly concave sides; typically at least 5µm long.
Remarks - Stradner's holotypic drawing is parallel-sided with dimensions 5µm x 2µm, and thus provides a minimum standard for this subspecies. The oldest forms fitting this definition were recorded in the Chale Clay of the Isle of Wight (lower *forbesi* ammonite Zone), although *R.angustus parvus* is still the dominant form at this level. This first occurrence is still very much earlier than the basal Upper Aptian event recorded by previous authors. There are various possible explanations for this apparent diachroneity - previous authors may only have included even more elongate (length/width > 3?) forms in *R.angustus*, or they may have been looking at condensed sections. Whatever the reason, there are plenty of alternative datums in the Aptian and *R.angustus* is perhaps best abandoned as a primary marker.

Rhagodiscus angustus (Stradner) subsp. ***parvus*** nov. subsp.

Plate 6, Figs. 14 & 15 (LM).

1987 *Rhagodiscus angustus* (Stradner, 1963) Reinhardt, 1971; Thomsen, p.77, pl.16, figs.6-8 (EM).

Diagnosis - Small (<5µm long), oval-shaped rhagodiscid with a length/width ratio of < 2.5.
Description - These forms are typically about 4µm long and oval-shaped, with straight or slightly convex longer sides. As in the larger subspecies, a hollow spine base is supported by transverse bars, and the central area is floored by a granular plate.
Remarks - This is the obvious ancestor of *R.angustus angustus*, and forms transitional between these two subspecies are observed. Thus, the first occurrence of *R.angustus angustus* is difficult to pinpoint accurately, and of dubious worth. *R.angustus parvus* is, however, quite markedly different to the earlier occurring *R.pseudoangustus* (which is more similarly proportioned to *R.angustus angustus*), so it seems that these two species are unrelated (see remarks under *R.pseudoangustus*). The granular plate is often observed on the LM, even in cross-polarised light; this is hardly ever seen in

R.pseudoangustus. The long axial ends of both subspecies are clearly rounded; this is not usually the case in *R.pseudoangustus*.

Occurrence - Common throughout the Aptian of the North Sea area; this subspecies is particularly abundant in the few nannofossiliferous samples from the Atherfield Clay (*fissicostatus-forbesi* ammonite Zones).

Holotype - Thomsen, 1987, p.77, pl.16, fig.6 (EM).

Isotype - Thomsen, 1987, p.77, pl.16, fig.7 (EM).

Type locality & level - Well E-1 (Danish Sector of the North Sea), 8193'; basal Aptian - probably equivalent to the lower part of the *fissicostatus* ammonite Zone (just below a major influx of *W.britannica*).

Rhagodiscus asper (Stradner, 1963) Reinhardt, 1967

Plate 5, Figs. 10-13 (EM);
Plate 6, Figs. 3 & 6 (LM).

Remarks - The species concept applied here includes all medium-sized, elliptical and oval-shaped forms, with a fairly complete central granular membrane, and without a prominent four-part spine. This includes some oval, spined forms which other authors might have assigned to *R.splendens*. There is considerable variation in the relative width of the rim and central membrane, and the wider-rimmed *R.reightonensis* ((Taylor, 1978) Watkins in Watkins & Bowdler, 1984) cannot be reliably differentiated on the LM. Similarly, *R.eboracensis*, which Black (1971) differentiated from *R.asper* by its imperforate membrane, is regarded as synonymous with *R.asper*. A hollow central spine may be present; this arises from a circular base that appears as a narrow bright ring under crossed polars. The granular central membrane may be perforated by one or more cycles of relatively small holes; it is not, however, reduced to a skeletal meshwork of struts, as in *R.fenestratus*.

Rhagodiscus cepekii (Crux, 1987) comb. nov.

Plate 5, Fig. 7 (EM).

1987 *Chiastozygus cepekii* Crux, p.30, pl.1, figs. 1-3, 6 (EM); 19-20, *non* 18 (LM).
1989 *Chiastozygus cepekii* Crux, 1987; Crux, pl.8.5, figs.4-7 (EM); pl.8.12, figs.11-12 (LM), *non* figs.10, 13, 14 (LM).

Remarks - This species has only been observed on the SEM, and is probably indistinguishable from small specimens of *R.asper* on the LM, without very careful focusing - the side views illustrated by Crux (1987, 1989) belong to *Neoparhabdolithus*

sp.1. On the SEM, this species exhibits the imbricate wall and granular basal membrane typical of *Rhagodiscus* (see the proximal surface in Crux, 1989, pl.8.5, figs.6 & 7). The "cross-bars" supporting the broad central spine are analogous with similar spine supports in other rhagodiscids (e.g. *R.infinitus*, *R.pseudoangustus*). This species may have a very restricted range, since most of Crux's (1989) LM records were probably of *Neoparhabdolithus* sp.1. The only definite, SEM records of this species are from the *variabilis* ammonite Zone (or equivalent) of Speeton, Germany and Borehole 81/43.

Rhagodiscus fenestratus (Stover, 1966) comb. nov.

1966 *Zygolithus fenestratus* Stover, p.147, pl.3, figs.21 & 22C (LM); pl.8, fig.24.
1976 *Parhabdolithus asper* Stradner, 1963; Hill, pl.10, figs.6-15 (LM).
1989 *Rhagodiscus asper* (Stradner, 1963) Reinhardt, 1967; Crux, pl.8.8, figs.1-2 (EM).
1990 *Rhagodiscus* sp. aff. *R.asper* Mutterlose & Wise, p.350, pl.5, fig.14 (LM).

Description - A large, broadly elliptical rhagodiscid in which the granular basal membrane consists of a skeletal meshwork of struts; these struts enclose large concentrically arranged holes, and support a prominent central spine of circular cross-section.
Remarks - Most previous workers have included this form in *R.asper* but it is quite distinctive and potentially useful, first occurring in the Aptian. Black (1971) recombined and amended *Z.fenestratus* to include Barremian podorhabdids, but Stover's holotype is clearly a rhagodiscid.

Rhagodiscus infinitus (Worsley, 1971) Applegate *et al.* in Covington & Wise, 1987

Plate 5, Figs. 8 & 9 (EM);
Plate 6, Fig. 8 (LM).

Remarks - This large, distinctive species has two large openings along the major axis of its central area; these pores are circumscribed by thickened, birefringent bars that support a hollow central process. This appears to have been a warm-water preferring species - it occurs consistently (and often commonly) throughout the Valanginian-?Cenomanian of Tethyan sites (Thierstein, 1973; Covington & Wise, 1987; Applegate & Bergen, 1988), but is only recorded sporadically in the Valanginian-Aptian of the North Sea area. Rahman & Roth (1991) recently reassigned this species to Worsley's original (1971), monospecific genus, *Mitosia*, on the basis of a single Kimmeridgian/Tithonian specimen; however, their illustrated specimen would seem to belong to a different species.

Rhagodiscus nebulosus Bralower *et al.*, 1989

Remarks - This precursor of *Percivalia fenestrata* (Bralower *et al.*, 1989) was recorded very rarely in the Upper Ryazanian of Speeton. It is restricted to the mid-Berriasian-Valanginian of Tethys (Bralower *et al.*, 1989).

Rhagodiscus pseudoangustus Crux, 1987

1979 *Rhagodiscus* cf. *R.angustus* Perch-Nielsen, p.229, fig.3 (not illustrated).
1987 *Zeugrhabdotus? pseudoangustus* Bralower, Applegate, Covington & Wise in Covington & Wise, p.633, pl.8, figs.2-4 (EM & LM).

Remarks - The basal membrane (occasionally visible on the SEM), and often irregularly thickened wall of this species are characteristic of *Rhagodiscus*, so it is retained in this genus. Two varieties were recorded in the present study - one is highly distinctive, and a potentially useful marker (var.1), while the other (var.2) is very similar to *R.angustus angustus*, and rather detracts from the value of this Aptian marker species.

Rhagodiscus pseudoangustus var.1

Plate 5, Figs. 1-6 (EM);
Plate 6, Figs. 10 & 11 (LM).

1987 *Rhagodiscus pseudoangustus* Crux, p.35, pl.1, figs.4-5 (EM).
1989 *Rhagodiscus pseudoangustus* Crux, 1987; Crux, pl.8.13, figs.16-17 (LM).
1988 *Zeugrhabdotus pseudoangustus* Bralower, Applegate, Covington & Wise, 1987; Applegate & Bergen, p.326, pl.7, figs.11-12 (EM).

Description - A subrectangular variety of *R.pseudoangustus*, with an irregularly thickened wall. This aberrant rim construction results in a peculiar appearance under cross-polarised light - the extinction gyres are confined to the sharply curved corners of the rectangular wall, dividing it into four straight sections. The bipartite bridge/spine support is not always preserved, but the rim alone is sufficiently distinctive. The rectangular shape and relatively high wall ensure that this form is often encountered in side view (Plate 6, Fig. 11).
Remarks - This is a distinctive form, that is readily distinguished from *R.angustus*. It occurs very sporadically throughout the Hauterivian of the studied sections, becoming conspicuous for a short interval in the Lower Barremian, just before its apparent last occurrence. Applegate and Bergen (1988) recorded *Z.pseudoangustus* consistently up to a similar level on the Galicia margin - higher, sporadic occurrences may have been attributable to *R.pseudoangustus* var.2.

Rhagodiscus pseudoangustus var.2

Plate 6, Fig. 12A (LM).

1987 *Rhagodiscus pseudoangustus* Crux, pl.1, figs.16-17 (LM).
1989 *Rhagodiscus pseudoangustus* Crux, 1987; Crux, pl.8.13, figs.18-19 (LM).

Description - Elongate, long-elliptical to subrectangular variety of *R.pseudoangustus* with rounded ends and a regularly thickened wall.
Remarks - Except for its apparent lack of a granular membrane, this form is virtually indistinguishable from *R.angustus* on the LM. This form occurs sporadically throughout the Hauterivian and Lower Barremian, and outlasts *R.pseudoangustus* var.1. Bearing in mind the rarity of both types in the earlier part of their ranges, it is possible that var.2 survived until the earliest Aptian, to give rise to *R.angustus*. However, since the earliest Aptian forms of *R.angustus* are much less elongate than *R.pseudoangustus* these forms are certainly not conspecific.

Rhagodiscus reniformis Perch-Nielsen, 1973

Remarks - Rare, irregularly-shaped rhagodiscids were assigned to this species; these may be aberrant specimens of another species.

Rhagodiscus splendens (Deflandre, 1953) Verbeek, 1977

Plate 6, Fig. 9 (LM).

Remarks - Many authors have assigned any moderately large, approximately oval-shaped rhagodiscid with a clear central spine to this species, resulting in records down to the Valanginian. However, such Neocomian forms only differ from *R.asper* in having a slightly less-elliptical outline, and these forms were not differentiated in the present study. *R.splendens* is herein applied to large, oval-shaped forms with a prominent, flaring four-part spine-base (rather than a hollow circular spine-base, as sometimes observed on *R.asper*). No doubt transitional forms occur, but there is no problem in differentiating fully-developed *R.splendens* from *R.asper* on the LM. Thus defined, *R.splendens* does not occur before the Aptian.

Genus *Rucinolithus* Stover, 1966

Rucinolithus windleyae sp. nov.

Plate 21, Figs. 1-8 (EM & LM).

?1987 *Lithastrinus* sp. Bralower, p.298 (not illustrated)

Derivation of name - Named in honour of Dawn E. Windley, nannopalaeontologist.
Diagnosis - Polycyclolith consisting of two inclined cycles of broad, petal-like elements: a wider ?proximal cycle of about 9 regularly imbricate elements, and a ?distal cycle formed from a lesser number of irregularly overlapping elements.
Description (EM & LM) - Two inclined cycles of broad, petal-like elements join at the solid centre of the nannolith (there is no central diaphragm). The wider ?proximal cycle consists of about 9 sinistrally imbricate, broadly petalloid elements. The ?distal cycle consists of a lesser number of irregularly arranged elements, at least one of which projects distally, overlapping the other elements of this cycle. In proximal view on the LM this form appears as a large (7-9µm diameter), highly birefringent rosette, with imbricating, petalloid elements; distal focusing reveals the irregular distal cycle. In side view it exhibits a typical polycyclolithacean construction, with two cycles of inclined elements. The fairly high and irregular form of this species ensure that it is often encountered in oblique view on the LM, where it appears as a highly irregular, radiating birefringent body.
Differentiation - *R.windleyae* differs from *Lithastrinus* (as amended by Varol, 1992) in lacking a small central diaphragm. It is similar, and probably related to *Rucinolithus pinnatus* Bergen (1994), but this older species (mid-Tithonian to latest Berriasian) has only eight imbricate elements and lacks a well-developed, irregular distal cycle (it has instead a small element cycle surrounding a central perforation). This species is differentiated from the unrelated but light-microscopically similar *Assipetra terebrodentarius* by its larger size, and petalloid (rather than globular) habit.
Occurrence - Mid-Hauterivian to Lower Barremian of Borehole 81/43 and the Speeton section; rare through most of this range, but occasionally common in the Upper Hauterivian to basal Barremian of Borehole 81/43. Bralower (1986) recorded the first occurrence of "*Lithastrinus* sp." (which included the later-appearing *Assipetra terebrodentarius*) in the Upper Hauterivian of a number of Tethyan sites.
Holotype - Plate 21, Fig. 1.
Paratype - Plate 21, Fig. 4.
Type locality & level - Borehole 81/43 (southern North Sea), 41.16m (Upper Hauterivian).

Genus *Staurolithites* Caratini, 1963

(syn: *Vekshinella* Loeblich & Tappan, 1963)
(syn: *Vagalapilla* Bukry, 1969)
(syn: *Staurorhabdus* Noël, 1963)

Remarks - *Staurolithites* is the oldest genus proposed for muroliths with an axially oriented cross, and the other (widely used) genera listed above are considered invalid. This genus is used for elliptical coccoliths with a simple wall, and an axially (or approximately axially) oriented central cross. Such forms are only differentiated from *Chiastozygus* and *Zeugrhabdotus* by their axially oriented cross. As with *Chiastozygus* and *Zeugrhabdotus*, all species of *Staurolithites* are believed to have walls constructed from two cycles of elements. However the inner, proximally located cycle is often rudimentary, so that the wall can appear unicyclic through most of its height on the LM (and in distal view on the SEM). Other forms have a well-developed (high) inner wall cycle, and the rim appears bicyclic throughout its height. Thus the LM discernible unicyclicity/bicyclicity of the wall is not used as a criterion for generic subdivision, as has been attempted by Varol & Girgis (*in press*). It is often even more difficult to discern the number of cycles in the wall on the SEM, since specimens cannot be flipped over to examine both proximal and distal surfaces. The relative development of these wall cycles is one of the main criteria used to differentiate the various species. Peculiarities in the construction of the wall (in particular the relative inclination of the elements in the inner and outer cycles) result in other distinctive LM properties, e.g. differences in the birefringence of the two wall cycles, and spiral extinction patterns. The axially oriented central cross seems to be quite a conservative character - most species assigned to this genus are characterised by their distinctive rim structure, rather than the particular construction of the cross. As with *Chiastozygus* and *Zeugrhabdotus*, further specimen transfer studies are required to enable accurate characterisation of the various light-microscopically distinct forms.

Staurolithites angustus (Stover, 1966) Crux, 1991

Remarks - This species has an central cross that is offset slightly from the axes of the coccolith; the bars of this cross are split along their length and flare towards their juncture with the rim. It is first recorded in the Albian of the Heslerton Borehole.

Staurolithites crux (Deflandre, 1954) Caratini, 1963

Plate 2, Fig. 3 (LM).

(syn: *Vekshinella stradneri* Rood *et al.*, 1971)

Remarks - The definition of this species is rather confused, not least since it was originally described from the Eocene (Deflandre & Fert, 1954), but it is used here for all medium-sized elliptical forms with a simple wall, that is not discernibly bicyclic on the LM, and an axially aligned central cross. Small forms, less than 4μm long, were recorded as "small *Staurolithites* spp.".

Staurolithites dibrachiatus (Gartner, 1968) comb. nov.

Plate 2, Fig. 9 (LM).

1968 *Vekshinella dibrachiata* Gartner, p.30, pl.5, figs.23-24 (EM); pl.7, figs.8a-8b (LM); pl.22, fig.8 (EM).

1991 *Vagalapilla dibrachiata* (Gartner, 1968) Rahman & Roth, p.769, pl.1, figs.1-3; pl. 4, fig.7 (EM & LM).

Remarks - The category is used, on the LM, for forms with a unicyclic rim and broad, medianly split cross-bars. Such forms are rare, and were grouped with *Staurolithites crux* during counting.

Staurolithites elliptica (Gartner, 1968) comb. nov.

1968 *Vekshinella elliptica* Gartner, p.30, pl.17, fig.5 (LM); pl.25, fig.26-27 (EM); pl.26, fig.7 (LM).

1976 *Vagalapilla elliptica* (Gartner, 1968) Bukry, 1969; Hill, pl.12, figs.3-6 (LM); pl.15, figs.16-19 (EM).

Remarks - This species is amply illustrated by Hill (1976), who discussed the taxonomic problems caused by the poor type specimens of several species of *Staurolithites / Vekshinella / Vagalapilla.* It is characterised by its compact form, obviously bicyclic wall and relatively thick cross-bars. The cross-bars flare towards their central juncture, where they support the base of a hollow spine. This species is conspicuous in the Upper Aptian and Albian. It probably evolved from the similar *Staurolithites* sp.1.

Staurolithites gausorhethium (Hill, 1976) comb. nov.

1976 *Vagalapilla gausorhethium* Hill, p.157, pl.3, figs.25-30 (LM).

1991 *Chiastozygus curvus* Varol, p.221, fig.6, 1-5 (LM).

Remarks - This species has a cross that is offset slightly from the principle axes of the coccolith. The longer bar appears sigmoidal when it is oriented obliquely to the polarising directions. The wall appears unicyclic, with a strong spiral extinction figure. It is characteristic of the Albian-Cenomanian.

Staurolithites? glabra Jeremiah, *in press*

Plate 2, Fig. 15 (LM).

1966 *Coccolithus matalosus* Stover, p.153, pl.2, fig.2, *non* fig.1 (LM).
1972 *Staurolithites matalosus* (Stover, 1966) Cepek & Hay, 1969; Roth & Thierstein, p.479, pl.13, figs.6-11 (EM & LM; same specimen).
1973 *Vagalapilla matalosa* (Stover, 1966) Thierstein, pl.3, figs.15-18 (EM & LM; same specimen).
1987 *Vagalapilla matalosa* (Stover, 1966) Thierstein, 1973; Hill & Bralower, pl.1, fig.1a-c (LM).

Remarks - This species is only tentatively retained in *Staurolithites* and should possibly be reassigned to *Eiffellithus*. It is easily distinguished from *Acaenolithus/Broinsonia* by its smooth margin and outer wall (which flares quite markedly on the LM). It is distinguished from *Eiffellithus monechiae* and *Eiffellithus eximius* by the relatively simple appearance of its cross in cross-polarised light; the bars are relatively narrow, parallel-sided and lack any striations or median extinction line. See *Acaenolithus matalosus* for further discussion of the taxonomic chaos arising from different concepts of Stover's *Coccolithus matalosus.*
Occurrence - Bergen (1994) records the lowest occurrence of this species (*Vagalapilla* sp.A) in the Lower Aptian of S.E. France, but notes similar forms very rarely in the Upper Hauterivian. In this study, this species was recorded rarely in the Lower Aptian of the Heslerton Borehole and consistently throughout the Albian of this section. I also recorded indistinguishable forms rarely in the Hauterivian-Barremian of Speeton and Borehole 81/43. Bergen (1994) differentiates the (rare) Neocomian forms from the consistently occurring Aptian-Albian forms by the outline of their central opening - the earlier forms having elliptical central openings, and the later forms diamond-shaped central openings. These forms obviously need further study, but it seems that the Neocomian forms may belong to a different species.

Staurolithites mitcheneri (Applegate & Bergen, 1988) comb. nov.

Plate 2, Figs. 5 & 8 (LM).

1988 *Vekshinella mitcheneri* Applegate & Bergen, p.317, p.342, pl.23, figs.7-9 (EM & LM; same specimen)

Remarks - This species is characteristically very compact (with only very narrow central openings) with a thick, bicyclic wall, and stubby axial cross. It has not previously been described from the North Sea area, and is generally rare, but ranges from the Early Valanginian to the Early Aptian.

Staurolithites mutterlosei Crux, 1989

Plate 1, Figs. 7-9 (EM);
Plate 2, Figs. 6-7 (LM).

Remarks - This species has a wall composed of two equally birefringent cycles, separated by spirally arranged extinction gyres, and an offset central cross. It is similar to *S.gausorhethium*, but the longer bar of its cross appears straight rather than sigmoidally curved in cross-polarised light, and its rim exhibits a much stronger spiral extinction figure.

Occurrence - Lower Hauterivian to mid-Barremian of the North Sea area; several isolated occurrences in the Aptian of the Heslerton Borehole may have been reworked. Bergen (1994) records this species (fairly sporadically) in the Lower Valanginian to Lower Cenomanian of low-latitude sites.

Staurolithites sp.1

Plate 2, Fig. 4 (LM).

1989 *Staurolithites* sp. Crux, p.194, pl.8.12, figs.19-20 (LM).

Description (LM only) - Medium-sized (about 6μm long), elliptical form with a wall that appears clearly bicyclic in cross-polarised light. The two cycles of the relatively narrow wall are approximately equal in width, and the inner cycle is more birefringent (white) than the outer cycle (grey). The extinction pattern across the wall is diffuse (rather than spiral). A simple cross is aligned with the axes of the coccolith; the cross-bars are relatively narrow, parallel-sided and unstriate. There does not appear to be a significant central process.

Differentiation - This species is altogether more regularly proportioned than other species of *Staurolithites* with visibly bicyclic walls. It lacks the spiral extinction pattern

and off-centre cross of *S.mutterlosei*, and the wide inner wall cycle of *S? glabra*. Its wall and cross-bars are narrower and more regularly thickened than in *S.elliptica*.

Occurrence - This species was first recorded in the middle Valanginian of Speeton and Borehole 81/43; Upper Ryazanian records from Core 7B may have been overgrown specimens of *S.crux*. Crux (1989) recorded this form down to the Upper Ryazanian of Speeton, so it may have originated earlier. It is common throughout the Hauterivian-Barremian and ranges at least as high as the Lower Albian.

Genus *Stradnerlithus* Black, 1971

Remarks - This genus is used for elliptical/rhomboidal forms with a delicate rim composed of approximately vertically arranged elements, and at least six, radially arranged bars in the central area. All these forms are only weakly birefringent, and best viewed in phase contrast illumination.

Stradnerlithus geometricus (Górka, 1957) Bown & Cooper, 1989

1957 *Discolithus geometricus* Górka, pl.4, fig.8.
1971 *Actinozygus geometricus* (Górka, 1957) Rood *et al.*.
1971 *Corollithion geometricum* (Górka, 1957) Manivit.

Remarks - Despite the poor definition of Górka's Maastrichtian holotype, and the subsequent, more accurate, description of a similar six-spoked form from the Upper Cretaceous (*Corollithion ellipticum* Bukry, 1969), this species is applied here to medium-sized (c.5µm long), six-spoked forms, with a smooth-margined, weakly birefringent rim. These are rare in the studied material.

Stradnerlithus hexserratus (Worsley, 1971) comb. nov.

Plate 6, Fig. 12B (LM);
Plate 8, Figs. 6 & 8 (EM).

1971 *Ellipsochiastius hexserratus* Worsley, p.1319, pl.1, figs.24-26 (LM).
1989 *Stradnerlithus geometricus* (Górka, 1957) Bown & Cooper, 1989; p.91, pl.1, figs. 31 & 36 (EM & LM).
1991 *Corollithion geometricum* (Górka, 1957) Manivit, 1971); Mutterlose, pl.7, figs.8-10 (EM).
1991 *Corollithion ellipticum* Bukry, 1969; Bralower, fig.6, 39-40 (LM).

Remarks - This species, originally described from the Neocomian, is similar to *S.geometricus*, with six radial spokes in its elliptical central area, but is considerably smaller (2-3μm long) and has a serrate outline in cross-polarised light (this can be seen in Bralower, 1991). It is common to abundant in the Lower Hauterivian and Lower Barremian of Speeton and Borehole 81/43.

Stradnerlithus rhombicus (Stradner & Adamiker, 1966) Bukry, 1969

Plate 8, Fig. 1 (EM).

Stradnerlithus silvaradius (Filewicz *et al.*, 1977) Rahman & Roth, 1991

Plate 8, Fig. 3 (EM);
Plate 9, Fig. 11 (LM).

1977 *Corollithion silvaradion* Filewicz *et al.* in Wise & Wind, p.310, pl.62, figs.2-6 (EM); pl.63, figs.5, 6 (LM).
1984 *Nodosella silvaradion* (Filewicz *et al.*, 1977) Perch-Nielsen, p.400, Fig.73.17 (EM).

Remarks - This species was originally described from the Aptian of the Falkland Plateau, but is restricted to the Valanginian and Lower Hauterivian of the Boreal area. It appears similarly restricted to the Valanginian-Hauterivian of Tethyan Sites (Applegate & Bergen, 1988; Bergen, 1994), although it ranges higher, into the Upper Hauterivian at these latitudes (Bergen, 1994). Neocomian forms appear virtually identical, on the SEM, to the Aptian holotype but, nevertheless, this may be an example of iterative evolution. The Late Jurassic specimens illustrated by Rahman & Roth (1991) have a crenulate outer margin, and probably belong to a different species.

Genus ***Tegulalithus*** Crux, 1986

Tegulalithus septentrionalis (Stradner, 1963) Crux, 1986

Remarks - This species resembles *Nannoconus* in cross-polarised light, but is easily differentiated in phase contrast, and in side view (its relatively high, quadrate form ensures that about one third of specimens are observed in highly distinctive side view). The side views display strongly concave proximal and distal plates joined by a wall of approximately vertically oriented elements. Rather like *Nannoconus abundans*, it shows considerable variation in size and in the development of flanges (formed by the proximal and distal plates overhanging the wall); however, unlike *N.abundans*, the proximal and

distal flanges are always equally developed. Based on the development of these flanges, two varieties are distinguishable on both LM and SEM. LM observations indicate that the ranges of these forms are concurrent, and they are recorded together on the range charts.

Occurrence - Upper Hauterivian (*speetonensis-gottschei* ammonite Zones) of the North Sea area, and the Barents Sea; later records from the North Sea area are due to reworking and/or misidentification of nannoconids (see also *Nannoconus pseudoseptentrionalis*). Roth (1983) recorded rare *Lithastrinus septentrionalis* from the Upper Hauterivian (redated here) of DSDP Site 534, in the western North Atlantic. Bralower (1989) recorded this species from the ?Hauterivian and Albian of California, but the Albian occurrences must surely be *Tegulalithus tessellatus*. Varol (1991) reported *T.septentrionalis* from the Hauterivian of Indonesia, and Silvia Gardin (*pers. comm.*) has recently found it in the Hauterivian parastratotyes of the Vocontian Trough. Thus, this short-ranging species had a wide geographical distribution; the relative lack of records from low latitude sections may be due to condensation.

Tegulalithus septentrionalis var.A

Plate 19, Figs. 9-13 (EM);
Plate 20, Figs. 11-13 (LM).

Description - This variety includes those classically developed forms whose proximal and distal plates overhang the wall elements, forming flanges. In end view under cross-polarised light the margin of the test appears ragged.

Tegulalithus septentrionalis var.B

Plate 19, Figs. 14 & 15 (EM);
Plate 20, Fig. 14 (LM).

Description - Resembles var.A in most respects, but lacks proximal and distal flanges. Thus the nannolith appears regularly scalloped in end view (each point on the scalloped margin represents a wall element). There may be an axial perforation through the centre of both plates, but this could be a dissolution feature. Size is variable (c.3-5μm diameter), but generally smaller than var.A.

Remarks - It is unlikely that this form is a dissolution product of var.A, since it never shows any vestiges of terminal flanges, and occurs in samples with abundant, pristine specimens of var.A.

Tegulalithus tessellatus (Stradner, 1968) Crux, 1986

Remarks - This species appears similar to *T.septentrionalis* var.A on the LM but is differentiated, in plan view, by a having a clear central perforation. It has never been seen (nor is it illustrated) in side view, but Stradner's holotypic TEMs and those of Black (1973) show that its proximal/distal surfaces have a much less regular ultrastructure than those of *T.septentrionalis*. The species is, in any case, separated in range from *T.septentrionalis* by three stages of the Lower Cretaceous.

Occurrence - Documented from the Upper Albian (*inflatum* ammonite Zone) of England by Black (1973), Crux (1991) and Jeremiah (*in press*), and from this level within the Norwegian sector of the North Sea by Varol (1992). In the present study, this species was recorded in the Albian of the Heslerton Borehole, and in a spot sample (Albian) from the U.S.A..

Genus ***Tegumentum*** Thierstein in Roth & Thierstein, 1972

(Type species: *Tegumentum stradneri* Thierstein in Roth & Thierstein, 1972)

Remarks - The forms assigned to this genus appear similar to *Eiffellithus* on the LM, but are differentiated on the SEM by having an inner wall cycle of clearly imbricate elements and lath-formed (rather than fibrous) cross (see Plate 3). Neocomian species of *Eiffellithus* have often been misassigned to this genus, as *Tegumentum striatum* (= *Eiffellithus striatus*), or misidentified as *Tegumentum stradneri.* Furthermore, *Tegumentum stradneri* has been consistently misused for other Neocomian forms which are here assigned to *Tegumentum bergeni* (sp. nov.). *T.stradneri*, as described by Thierstein, differs from Neocomian representatives of this genus in having a more strongly imbricate inner wall cycle that yields a spiral extinction pattern. In the present study, such forms were only encountered rarely in the uppermost Barremian of the Heslerton Borehole, which fits with Thierstein's Late Barremian to Maastrichtian range. The 'proximal rim' (= cycle of small elements attached to the proximal side of the wall) which Thierstein (in Roth & Thierstein, 1972) noted on *T.stradneri* has not been identified on Neocomian species of *Tegumentum*, but these are poorly known in proximal view.

Tegumentum bergeni sp. nov.

Plate 3, Figs. 10-12 (EM);
Plate 4, Figs. 5-7 & 9-10 (LM).

Derivation of name - Named in honour of Dr. James Bergen, nannopalaeontologist.

Diagnosis - A species of *Tegumentum* whose wide, dextrally imbricate inner wall cycle is composed of subquadrate elements that are separated by radially or anticlockwise inclined sutures (when viewed from the distal side).

Description (EM) - Medium-sized (3-6μm long), elliptical murolith with a bicyclic wall and an open central area spanned by a diagonally oriented central cross. The narrow outer wall cycle is constructed from non-imbricate, tabular elements. A wide inner cycle is constructed from 25-30 subquadrate elements, which are dextrally imbricate with radially or (more often) anticlockwise inclined sutures. The lath-formed cross-bars may be straight or sigmoidally curved, joining the inner margin of the rim tangentially; the bars do not overlap the distal surface of the rim, but are joined to the inner margin or proximal side of the inner wall cycle. A short, solid, distal process arises from the distally elevated juncture of the cross.

Description (LM) - The rim exhibits an extinction pattern reminiscent of *Eiffellithus*, with a very weakly birefringent narrow outer cycle and strongly birefringent (white) inner cycle. The cross-bars are moderately birefringent and appear sigmoidally curved in cross-polarised light, with pointed terminations.

Differentiation - This species differs from *Tegumentum stradneri* in having its inner wall composed of fewer, larger, subquadrate elements whose sutures are radially or anticlockwise inclined, rather than clockwise inclined (compare the SEMs in Plate 3 with Thierstein's paratype (in Roth & Thierstein, 1972, pl.1, fig.11)). This subtle difference in ultrastructure results in a different LM extinction pattern; *T.stradneri* displays spirally arranged extinction gyres, while those of *T.bergeni* are approximately radially disposed (compare the LMs in Plate 4 with Thierstein's LMs (in Roth & Thierstein, 1972, pl.1, figs.8-10 & 13-15) . *T.bergeni* is differentiated from contemporary species of *Eiffellithus* by the distinctive arrangement of its central cross-bars; these appear sigmoidally curved in cross-polarised light, with pointed terminations.

Occurrence - Cosmopolitan; Upper Valanginian to uppermost Albian or basal Cenomanian (first occurrence of *"T.stradneri"* from Applegate & Bergen, 1988; last occurrence of *"T.striatum"* from Jeremiah, *in press*).

Holotype - Applegate & Bergen (1988), p.337, pl.18, figs.1-3 (SEM & LMs; same specimen).

Isotype - Plate 3, Fig. 10 (EM).

Type locality & level - ODP Site 638B (Galicia Margin), 23R-6, 58-59cm (Upper Hauterivian).

Remarks - Previous authors have assigned this species to *Tegumentum stradneri* or *Tegumentum striatum* (=*Eiffellithus striatus*). Applegate and Bergen (1988, pl.18, figs.1-3) provided SEM and LMs of a specimen of *"T.stradneri"* which is clearly different to Thierstein's type specimens (these are also figured on both SEM and LM). All this confusion may be partly due to the variable nature of *T.bergeni*, which includes forms transitional with *T.octiformis*. Three light-microscopically distinguishable varieties of

this species were recognised; others may not wish to distinguish these varieties but, although they are apparently intergradational in form, they do differ considerably in range. These varieties are regarded as informal.

Tegumentum bergeni var. *bergeni*

Plate 3, Figs. 10-12 (EM);
Plate 4, Figs. 5-6 & 9 (LM).

1982 *Tegumentum stradneri* Thierstein, 1972; Taylor, pl.4.7, fig.21 (LM).
1987 *Tegumentum stradneri* Thierstein, 1972; Jakubowski, pl.1, figs.18-19 (LM).
1988 *Tegumentum stradneri* Thierstein, 1972; Applegate & Bergen, pl.18, figs.1-3 (EM & LM).
1989 *Tegumentum stradneri* Thierstein, 1972; Bralower *et al.*, pl.II, figs.14-15 (LM).
1989 *Tegumentum striatum* (Black, 1971) Crux, pl.8.5, fig.1 (EM); pl.8.12, figs.1-4 (LM).

Characteristics - This variety includes the type specimens of the species, and is characteristically medium-sized (4-6μm long) with a relatively broad inner wall cycle and cross-bars that appear straight or (more usually) sigmoidally curved in cross-polarised light. The cross-bars may be recurved partly around the inside of the wall, but the recurved portions do not join to form a figure of eight, as in var. *quasioctiformis*.
Occurrence - This is a long-ranging variety (Upper Valanginian to uppermost Albian or basal Cenomanian); it is especially conspicuous, and rather larger, in the Aptian.

Tegumentum bergeni var. *minor*

Plate 4, Fig. 7 (LM).

Characteristics - This variety is characteristically small in size (2-4μm long). It is only known on the LM and may be indistinguishable from var. *bergeni* on the SEM, except by size. The weakly birefringent cross-bars do not appear to overlap the birefringent inner rim cycle, and are not visibly recurved around the inner margin of the rim (unlike var. *quasioctiformis*). This form appears quite similar to the much later appearing *Helicolithus trabeculatus*, but is smaller and more delicately constructed.
Occurrence - This form is virtually confined to the Lower Barremian (*variabilis-rarocinctum* ammonite Zones) of Speeton and Borehole 81/43, and may be a useful secondary marker. It was also recorded in the Lower Barremian of Germany and ,as isolated rims, in the dissolution affected assemblages of the Barents Sea.

Tegumentum bergeni var. *quasioctiformis*

Plate 4, Fig. 10 (LM).

1989 *Tegumentum octiformis* (Kothe, 1981) Crux, pl.8.12, figs.6-7 (LM).

Characteristics - A medium-sized (c.5-6µm long) variety with a narrow inner wall cycle and sigmoidally curved cross-bars that extend around the inner margin of the rim (beneath the inner, imbricating wall cycle) to join up and describe a figure-of-eight. This variety is similar to *T.octiformis*, but its cross-bars are still sufficiently elevated above the rim so that it is impossible to focus on the entire figure-of-eight simultaneously, and the birefringent inner wall is wider than in *T.octiformis*.
Occurrence - Basal Hauterivian (or Upper Valanginian?) to Albian; this form is much longer-ranging than the closely-related *T.octiformis*.
Remarks - This variety includes forms transitional between *T.bergeni* and *T.octiformis*. These forms were "split" off in order to narrow the concept of *T.octiformis* so that it might be biostratigraphically useful.

Tegumentum octiformis (Kothe, 1981) Crux, 1989 emend.

Plate 3, Fig. 13 (EM);
Plate 4, Figs. 8 & 11 (LM).

?1981 *Chiastozygus octiformis* Kothe, p.20-21, pl.2, fig.2 (not available).
1982 *Chiastozygus striatus* Black, 1971; Taylor, pl.4.4, fig.12 (EM).
1989 *Tegumentum octiformis* (Kothe, 1981) Crux, p.196, pl.8.5, figs. 2-3 (EM).

Emendation - This species concept is narrowed to include only those forms with a narrow inner wall cycle, in which the entire figure-of-eight formed by the extended cross-bars can be resolved in a single plane of focus, on the LM. This amended definition probably corresponds with the "regular *Tegumentum octiformis*" of Crux, 1989 (p.166-7). The SEM reveals that the dextrally imbricate elements of the inner wall have clockwise inclined sutures, rather like *T.stradneri*.
Occurrence - Common in the Hauterivian-Barremian of the North Sea area; this species ranges from the Early Hauterivian *regale* ammonite Zone to the latest Barremian (?*bidentatum* Zone). The closely-related *T.bergeni* var. *quasioctiformis* appears earlier (earliest Hauterivian?) and ranges considerably higher than *T.octiformis*. This appears to be an endemic Boreal species.

Genus *Triquetrorhabdulus* Martini, 1965

Remarks - Perch-Nielsen (1988) tentatively assigned the Valanginian species *T? shetlandensis* to the genus *Triquetrorhabdulus*, which had only previously been applied to Oligocene-Miocene nannoliths. Well-preserved specimens of *T? shetlandensis* appear remarkably similar to the Miocene species *Triquetrorhabdulus auritius* Stradner & Allram (1981) and are here considered to belong to this genus. Other apparently triradiate, highly birefringent bodies were recorded from the Hauterivian to basal Barremian of Borehole 81/43; these are only tentatively assigned to *Triquetrorhabdulus* (as *Triquetrorhabdulus?* sp.1). These forms may be related to the Albian genus *Ceratolithina*; *Ceratolithina cruxii* has a similar, bladed construction, and seems to have been the ancestor of the more dissimilar *Ceratolithina hamata* and *Ceratolithina bicornuta*. These large and birefringent forms have been largely overlooked until recently, probably because their very size and birefringence was suggestive of an inorganic, crystalline origin. Thus, it is possible that some hitherto ignored species of *Triquetrorhabdulus* survived into the Aptian or Early Albian, to give rise to *C.cruxii*. This evolutionary scenario would seem to have been re-iterated in the Neogene - Perch-Nielsen (1985) suggested that Miocene forms of *Triquetrorhabdulus* gave rise to the horseshoe-shaped genera *Ceratolithus* and *Amaurolithus*.

Varol & Girgis (1994) have proposed a benthonic, ascidian origin for *T.shetlandensis*, but its wide geographical distribution (Barents Sea to S.E. France) and the apparent synchroneity of its first occurrence in every section make this seem unlikely. Coccolithophorids are certainly capable of producing such peculiar nannoliths, since the rather similar *Ceratolithus* is found encircling the protoplasts of living coccolithophorid cells (Norris, 1965). Furthermore, recent data (Bown, 1993) has shown that the similarly constructed Albian genus *Ceratolithina* was widely distributed, suggesting a similar planktonic origin. Other spicular bodies, of probable ascidian origin, are discussed at the end of this chapter.

Triquetrorhabdulus shetlandensis Perch-Nielsen, 1988

Remarks - This conspicuous species has been overlooked by most nannofossil specialists since when overgrown, as it generally is in the carbonate-rich basal Valhall Formation of the North Sea, it resembles a crystal of inorganic origin. Perch-Nielsen's (1988) illustrated specimens are, unfortunately, quite heavily overgrown, although the holotype shows the characteristic diamond-shaped profile. Well-preserved specimens display three triangular blades, that are widest towards the blunter end of the angular, diamond-shaped body. The whole nannolith is highly birefringent when oriented at 45° to the polarising directions (when the vertically standing blade reaches blue birefringence),

and extinct when oriented parallel with the polarisers. Overgrown specimens tend be more rounded, but can still be recognised by means of the third, vertically standing blade. Heavy overgrowth obscures even this diagnostic feature - elongate teardrop-shaped objects lacking a clear third blade were recorded as ?*Triquetrorhabdulus* sp.. Two varieties are recognised in this study; their separation is based on size.

Occurrence - Valanginian of the North Sea, Barents Sea, and S.E. France. Perch-Nielsen (1988) reported *T.shetlandensis* from the Lower Valanginian to Lower Hauterivian of Speeton and the North Sea, but gave no bed numbers from Speeton. This species' range was difficult to constrain, due to extreme condensation of the Valanginian, but the highest (possibly reworked) record is from the basal Hauterivian Bed D2D (several specimens were recorded in this remanié horizon which contains derived Upper Valanginian macrofossils). Perch-Nielsen might have included *Triquetrorhabdulus?* sp.1 with this species, thus extending its range into the Hauterivian. This species has recently been observed in the Lower Valanginian (*campylotoxum* ammonite Zone) of S.E. France (*pers. obs.*).

***Triquetrorhabdulus shetlandensis* large var.**

Plate 26, Figs. 10-12 (LM).

1988 *Triquetrorhabdulus? shetlandensis* Perch-Nielsen, p.37, pl.1, figs.15-16 (LM).

Description - Large, elongate (15-25µm long) form of *T.shetlandensis*; the length of the nannolith is generally greater than or equal to twice its maximum width (which is located towards the blunter end).

Fig. 2.11 - Optical characteristics of the Neocomian forms of *Triquetrorhabdulus* (in cross-polaised light).

Triquetrorhabdulus shetlandensis small var.

Plate 26, Fig. 13 (LM).

Description - Small, relatively short (6-8μm long) form of *T.shetlandensis*, with a low length/width ratio (the nannolith is only slightly longer than its maximum width).
Remarks - No specimens between these two size ranges were observed. The small variety was only recorded in the Valanginian of Borehole 81/43. Further studies of thicker Valanginian sequences may show that the two varieties are gradational. A group of three aligned specimens was observed (Plate 26 , fig. 13) in a sample in which *T.shetlandensis* was quite rare.

Triquetrorhabdulus? sp.1

Plate 27, Figs. 11 & 12 (LM); ?Figs. 13 & 14 (EM).

Description - A large (up to 30μm long), elongate, triradiate nannolith similar to *T.shetlandensis*, but triangular rather than diamond-shaped in outline. This form occasionally appears slightly fibrous in cross-polarised light, a character not observed in *T.shetlandensis.*
Occurrence - Mid-Hauterivian to basal Barremian of Borehole 81/43; rare through most of this interval, but occurs quite consistently in the Upper Hauterivian, within the range of *Tegulalithus septentrionalis.*

Genus *Tubodiscus* Thierstein, 1973 emend. Grün in Grün & Allemann, 1975

Tubodiscus jurapelagicus (Worsley, 1971) Roth, 1973

Plate 14, Figs. 7 & 10 (LM & EM).

Remarks - Although it is likely that the original species concept of Worsley (1971) was more similar to *Tubodiscus verenae*, these two species are retained, and the differential diagnoses of Applegate & Bergen (1988), Bralower *et al.* (1989) and Bralower (1991) are applied. Thus *T.jurapelagicus* has a relatively short central collar, which exhibits only grey or white birefringence. This large and conspicuous species has been included with the similarly proportioned *Manivitella pemmatoidea* by most previous Boreal workers; it is nevertheless easily distinguished on the LM by its flaring collar, and the lack of ornament on its distal shield. Applegate & Bergen (1988) recorded the highest occurrence of *T.jurapelagicus* in the Barremian of the Galicia Margin, but this event has never been

utilised. I recorded this species up to the mid-Barremian of Speeton, so this last occurrence could be a useful event.

Tubodiscus verenae Thierstein, 1973

Plate 14, Fig. 8 (LM).

Remarks - In proximal/distal view on the LM this species is distinguished from *T.jurapelagicus* by its highly birefringent (yellow-orange) collar; this is much taller than in *T.jurapelagicus* and extends to a much higher level of focus than the rim. No doubt gradational forms occur (Applegate & Bergen, 1988), but these were not encountered. Grün (*in* Grün & Allemann, 1975) amended *T.verenae* to include various other species of *Tubodiscus* and *Manivitella*, but this emendation is not accepted here. Boreal nannofossil workers have tended to overlook this species entirely, due to its extreme rarity at higher latitudes, but Tethyan workers have placed considerable importance on the species ever since Thierstein (1973) established that it was restricted to the Valanginian. Applegate & Bergen (1988), however, recorded this species rarely but consistently up to the Upper Hauterivian of the ODP Site 638. Bralower (1991) was dubious of this extended range, but on reinvestigation of Site 638 he found *T.verenae* almost as high as these authors. He nevertheless remained dubious, disputing the age assignments of Applegate & Bergen and invoking reworking to explain the apparently extended range. Bralower (1991) recorded *T.verenae* rarely in Borehole 81/43 up to a level which microfaunal and lithostratigraphical correlation with the Speeton section indicated to be of Hauterivian age. Based on this last occurrence, which he still believed to be a reasonable estimate for the Valanginian-Hauterivian boundary, Bralower proposed that this stage boundary may have been placed up to 11m too high at Speeton. This study revealed *T.verenae* 15m higher in Borehole 81/43 than Bralower's last occurrence, in strata of indisputable Late Hauterivian age; several very definite specimens (Plate 14) were recorded in each of two closely spaced samples. There is no question of reworking of these specimens, due to the extreme rarity of *T.verenae* in the underlying section. Similarly, Bergen (1994) has recorded this species up to the Late Hauterivian *sayni* ammonite Zone of Vergons, S.E. France. Furthermore, there is no doubt that Applegate & Bergen's (1988) highest occurrence of *T.verenae* was in the Upper Hauterivian - they recorded this event above the highest occurrence of *C.cuvillieri* and the highest consistent (non-reworked) occurrence of *E.striatus*. Thus, there is no doubt that *T.verenae* did linger on into the Upper Hauterivian, and its last occurrence cannot be used to mark the top of the Valanginian. Taylor (1982) recorded *T.verenae* up to the Upper Albian of the North Sea area, but undoubtedly included both *T.jurapelagicus* and *Tubodiscus parvus* in her concept of this species.

Tubodiscus parvus sp. nov.

Plate 14, Figs. 1-6 (LM & EM).

1989 *Manivitella pemmatoidea* (Deflandre) Thierstein, 1971; Bralower *et al.*, p.220, pl.VI, figs.15-17 (LM & EM; same specimen).

Derivation of name - Latin, *parvus*, meaning small.
Diagnosis - Small species of *Tubodiscus*, lacking a markedly elevated collar.
Description (LM) - Medium-sized (6-8μm long), elliptical placolith with a wide, open central area surrounded by a birefringent central tube that is not discernibly elevated above the rim (the entire coccolith can be resolved in one plane of focus). The rim itself is only weakly birefringent (grey) and appears unornamented in cross-polarised light.
Description (EM) - This species is constructed along tubodiscacean format, with a relatively short, vertically projecting proximal collar, and an unornamented distal shield.
Differentiation - *T.parvus* is differentiated from the very similar *T.jurapelagicus* by its smaller size (<9μm long) and relatively low central collar; these two species are readily differentiated on the LM, but virtually inseparable on the SEM (other than by measurement). It is differentiated from *Manivitella pemmatoidea* by its smaller size, and its altogether simpler and unornamented appearance in cross-polarised light. *Manivitella pecten* Black, 1973 is very much larger than *T.parvus* (averaging c.14μm long) and lacks the elevated collar of *T.jurapelagicus.*
Occurrence - Mid-Valanginian to Albian of the North Sea area; rare until the Late Hauterivian, but common from the Early Barremian onwards. This is by far the most common tubodiscacean in the North Sea area.
Remarks - This form is much longer-ranging than *T.jurapelagicus*, and thus worth differentiating. Bralower *et al.* (1991) illustrate this species (which they believed to represent an overgrown specimen of *M.pemmatoidea*) in the same plate as *T.jurapelagicus* and *T.verenae.*
Holotype - Plate 14, Fig. 5 (LM).
Isotype - Plate 14, Fig. 6 (LM).
Type locality & level - Borehole 81/43 (southern North Sea), 7.12m (Lower Barremian).

Genus *Watznaueria* Reinhardt, 1964

Remarks - *Ellipsagelosphaera* Noël, 1965 is here regarded as a junior synonym of *Watznaueria*, but those forms with an inner tube cycle could be assigned to the former genus. Most of the species of *Watznaueria/Ellipsagelosphaera* were described on the TEM/SEM, and their differentiation is relatively difficult on the LM. Thus LM workers

have tended to lump most forms of *Watznaueria* into *"W.barnesae"*. In this study, a number of forms not generally recognised on the LM were recorded, so their optical characteristics are described below. The identity of most of these forms could not be confirmed on the SEM, so some are named rather tentatively.

Watznaueria barnesae (Black, 1959) Perch-Nielsen, 1968

Plate 11, Fig. 18 (LM);
Plate 12, Fig. 6 (EM).

LM characteristics - The extinction gyres meet in the solid centre of the coccolith, forming a swastika-like extinction pattern, and do not separate on rotation.

Watznaueria biporta Bukry, 1969

LM characteristics - A large form with two well defined pores aligned in the long axis of its central area. The pores are separated by a bar that is optically continuous with the rim.
Remarks - This species has not been observed in material older than Albian; workers recording it from Neocomian sections probably included *W.communis* in their concept.

Watznaueria britannica Stradner, 1963

Plate 11, Fig. 21 (LM);
Plate 12, Fig. 2 (EM).

LM characteristics - A central perforation is spanned by a disjunct bar, oriented at a low angle to the minor axis of the coccolith.

Watznaueria communis Reinhardt, 1964

Plate 11, Fig. 19 (LM).

LM characteristics - The extinction gyres separate into two V-shaped figures when the axes of the coccolith are oriented at 45° to the polarising directions; when aligned with the polarisers the gyres meet at the centre of the coccolith, which is solid as in *W.barnesae*.
Remarks - Central perforations are not visible on the LM, but it is probable that two small perforations lie in the long axis of the central area, causing separation of the extinction gyres; thus Grün and Allemann (1975) probably misidentified this form on the

SEM as *W.biporta*. Occasional forms with very widely separated extinction gyres are encountered - these might be attributable to *Watznaueria supracretacea* (Reinhardt, 1965) Wind & Wise in Wise & Wind, 1976. The counted figures of *W.barnesae* include a certain component of *W.communis*, since it was not practicable to rotate every specimen during counting.

Watznaueria ?fasciata Wind & Cepek, 1979

Plate 11, Figs. 15 & 16 (LM).

LM characteristics - A small (about 4μm long), elliptical coccolith in which the extinction gyres are deflected parallel to the margins of the relatively small central area, which is moderately-weakly birefringent but contains no discernible structure (even in phase contrast). The deflection of the extinction gyres is best viewed with the coccolith oriented at 45° to the polarisers.

Remarks - In well-preserved material this form is easily identified on the LM. However the species' identity could not be confirmed on the SEM, since no definite, complete specimens of *W.fasciata* (which is characterised by an arrangement of transverse bars across its central area) were identified. Nevertheless, the LM proportions match those of *W.fasciata.* Forms in which dissolution had caused loss of the central structure were recorded as "small indet. *Watznaueria*". SEMs of such dissolution modified forms are often illustrated in the literature as *W.ovata.*

Occurrence - This species has only previously been described on the SEM so little range data exists. It was recorded throughout the Upper Ryazanian to Aptian, but is especially common in the Upper Hauterivian and Lower Barremian. It has previously been recorded from both Atlantic margins (Wind & Cepek, 1979; Covington & Wise, 1987).

Watznaueria fossacincta (Black, 1971) Bown in Bown & Cooper, 1989

Plate 11, Fig. 20 (LM);
Plate 12, Figs. 3-5 (EM).

LM characteristics - This form has a clear, unbridged central perforation of relatively small width.

Remarks - Etched specimens of *W.barnesae* or *W.britannica* may be mistaken for this species; thus perforate specimens showing clear signs of dissolution were recorded as *Watznaueria* indet..

Watznaueria ovata Bukry, 1969

Plate 11, Fig. 17 (LM).

LM characteristics - This form has a wide, open central area, wider than the width of its rim. The rim is moderately birefringent and its outer margin is smooth.
Remarks - This may be a protococcolith of *W.barnesae* or *W.fossacincta.*

Watznaueria ?rawsonii Crux, 1987

Plate 12, Fig. 1 (EM).

LM characteristics - Small-medium sized (4-6μm long) coccolith with a wide central area (approximately the same width as the surrounding rim) which generally appears entirely empty, but is occasionally seen to contain a weakly birefringent, granular grille. Two cycles are visible in the rim, the inner cycle being markedly narrower. The rim exhibits white birefringence and has a serrate margin. In the absence of the central grille, this species is distinguished from *W.ovata* by its serrate margin, lower birefringence and by the relative proportions of the cycles of its rim.
Occurrence - This species was recorded throughout the Valanginian-Barremian, but was only recorded consistently in the Upper Hauterivian and Lower Barremian; it has only previously been recorded (on the SEM by Crux, 1987, 1989, and Thomsen, 1987) from this same interval, so it may have quite a restricted range.

Watznaueria **sp.1**

LM characteristics - A small (about 5μm long) form, similarly proportioned to *W.fossacincta*, but with vague transverse bar-like structures in its central area. The central structure is visible in both cross-polarised and phase contrast illumination, but poorly defined. The extinction gyres are radial, and not deflected as in *W.?fasciata.*
Occurrence - Recorded sporadically in the Lower Hauterivian and Lower Barremian.

Genus ***Zeugrhabdotus*** Reinhardt, 1965

Remarks - This genus is used for all muroliths with a bicyclic wall and a multi-lath bridge spanning the short axis. The inner cycle of the wall is generally restricted to the proximal side, and thus not always obvious. The bridge always consists of two laterally appressed, lath-formed bars; these may be fused and surmounted by a spine on the distal side, but the bipartite division is almost always obvious on SEMs of the proximal surface. American authors have tended to use the Tertiary genus *Zygodiscus* Bramlette & Sullivan, 1961 for many of these forms. However, bearing in mind the uncertain

phylogenetic relationship between Cretaceous and Tertiary "zygodiscids", it is thought best to use a separate name for the Mesozoic forms, and *Zeugrhabdotus* is the oldest well-defined genus proposed for such forms. The transversely-bridged murolith seems to be quite a conservative, basic morphotype and all Mesozoic forms are probably related. Thus, there is little point in distinguishing genera such as *Glaukolithus*, *Placozygus* and *Reinhardites*, and these are considered synonymous with *Zeugrhabdotus*. Similarly *Parhabdolithus*, which is often applied to such forms, is considered redundant for Cretaceous forms (see comments under *Neoparhabdolithus*). The various species of *Zeugrhabdotus* are distinguished using the following (LM) criteria:

(1) Size, and overall birefringence.

(2) The relative width of the wall, bridge and central openings.

(3) The (LM discernible) unicyclicity or bicyclicity of the wall; this reflects the height and development of the proximal wall cycle.

(4) The relative birefringence of the two wall cycles (in bicyclic species); this reflects the relative inclination of the elements in each cycle.

(6) The arrangement of extinction gyres across the rim (spiral or radial).

(5) Peculiarities in the construction of the bridge; in particular, the presence/absence of a central spine.

Most of these characters are rather subjective, and this has resulted in a great deal of variability in the species concepts of different authors, thus limiting the biostratigraphical potential of these species. An additional problem is that a number of Late Cretaceous species were defined using EM criteria that are entirely useless to the LM worker, e.g. using the number of elements in the distal wall cycle. Detailed same-specimen examination is thus required for unequivocal naming of certain forms. This was not undertaken in the present study, but every effort was made to accurately characterise the various species.

Zeugrhabdotus compactus (Bukry, 1969) comb. nov.

1969 *Zygodiscus compactus* Bukry, pl.34, figs.1-2 (EM).

Remarks - Recorded only very rarely in the studied material, and those few records may have been overgrown specimens of *Z.diplogrammus*. This species is differentiated from *Z.diplogrammus* by its more compact form, with a wider rim and thicker transverse bars.

Zeugrhabdotus diplogrammus (Deflandre, 1954) comb. nov.

Plate 10, Fig. 19 (EM);
Plate 11, Fig. 6 (LM).

1954 *Zygolithus diplogrammus* Deflandre in Deflandre & Fert, p.148, pl.10, fig.7.
1972 *Glaukolithus diplogrammus* (Deflandre in Deflandre & Fert, 1954) Reinhardt, 1964; Roth & Thierstein, pl.11, figs.1-5 (EM & LM; same specimen).
1976 *Zygodiscus diplogrammus* (Deflandre in Deflandre & Fert, 1954) Gartner, 1968; Hill, pl.12, figs.25-27 (LM); pl.15, figs.25-26 (EM).
non 1985 *Glaukolithus diplogrammus* (Deflandre in Deflandre & Fert, 1954) Reinhardt, 1964; Perch-Nielsen, p.407, fig.82.4-5 (LM).

Remarks - Characterised by its simply constructed bridge, which consists of two closely appressed but unfused bars, without any central process. This species has been well illustrated by Roth and Thierstein (1972) and Hill (1976).
Occurrence - Mid-Valanginian to Maastrichtian; the first occurrence of this form is a potentially useful event.

Zeugrhabdotus 'elegans' (Gartner, 1968 emend. Bukry, 1969) comb. nov.

Plate 11, Fig. 7 (LM).

1968 *Zygodiscus elegans* Gartner, p.32, pl.10, figs.3-6 (EM); pl.12, figs.3-4 (LM); pl.27, fig.1 (EM).
1969 *Zygodiscus elegans* Gartner, 1968 emend. Bukry, p.59, pl.34, figs.6-8 (EM).
1972 *Glaukolithus elegans* (Gartner, 1968 emend. Bukry, 1969) Thierstein in Roth & Thierstein, p.437, pl.10, figs.16-20 (EM & LM; same specimen).
1973 *Zygodiscus elegans* Gartner, 1968 emend. Bukry, 1969; Thierstein, pl.2, figs.8-11 (EM & LM; same specimen).

Remarks - *Z.elegans*, as described by Gartner (1968), is clearly synonymous with *Reinhardites anthophorous* (Deflandre, 1959) Perch-Nielsen, 1968. Nonetheless, Bukry (1969) amended the description of this species to distinguish it (on the EM) from *Zygodiscus sisyphus*. Having conducted a same specimen EM and LM study, Roth & Thierstein (1972) and Thierstein (1973) applied Bukry's amended concept to forms essentially similar to *Z.diplogrammus* but with a central process. Thus the definition of this species is so convoluted that it should probably be abandoned altogether. Nevertheless, recent workers have tended to use this species as a dump category for all types of medium-sized *Zeugrhabdotus*. A similarly broad concept was applied here during logging of the first few sections (notably Speeton), but in Borehole 81/43 the narrower concept of Roth & Thierstein, 1972 was used. Thus defined, as a *diplogrammus*-lookalike with a spine, this species is rare in the studied material.

Zeugrhabdotus embergeri (Noël, 1959) Perch-Nielsen, 1984

Plate 10, Figs. 7-9 (EM & LM);
Plate 11, Figs. 4 & 5 (LM).

Remarks - There is no problem in identifying this large and birefringent species; Bralower *et al.* (1989) showed that early forms are transitional with *Z.erectus* in the uppermost Jurassic, but the fully-developed Cretaceous forms are very distinctive.

Zeugrhabdotus erectus (Deflandre in Deflandre & Fert, 1954) Reinhardt, 1965

Plate 10, Figs. 4-6 (EM & LM);
Plate 11, Figs. 2-3 (LM).

1989 *Zygodiscus erectus* (Deflandre in Deflandre & Fert, 1954); Bralower *et al.*, p.207, pl.II, figs.1-8 (EM & LM; same specimen).

Remarks - Recent palaeoceanographical studies have tended to lump all small zeugrhabdotids into this category, giving the impression that the species ranges throughout the Cretaceous. In this study, the concept was limited to small-medium (4-7µm long), simply constructed forms with birefringent bridges. These forms are constructed similarly to *Z.embergeri*, but have a much narrower inner wall cycle (the rim appears unicyclic on the LM). The main characteristic, however, is that the bridge is much more brightly birefringent (white) than the rim (grey). Thus limited, this a potentially useful marker, which last occurs in the Upper Hauterivian of Tethys (Bergen, 1994). In the North Sea area this species is, however, very rare in its upper range. It is very common, and rather larger, in the Kimmeridgian of Borehole 81/43.

Zeugrhabdotus* sp. cf. *Z.erectus

?Plate 10, Fig. 17 (EM).

Remarks - Forms similar to *Z.erectus*, but with less massively constructed (less birefringent) bridges were recorded in this category. These are mostly quite similar to *Tranolithus gabalus*, but have a less blocky bridge with a distinct spine base. This category includes forms assigned to *Zeugrhabdotus* species A by Bergen, 1994.

Zeugrhabdotus noeliae Rood *et al.*, 1971

Plate 10, Figs. 1-3 (EM & LM);
Plate 11, Fig. 1 (LM).

Remarks - This is the smallest, and by far the most abundant species of *Zeugrhabdotus*. It is generally ignored by biostratigraphers because of its small size and long range (Callovian-Maastrichtian), but it forms regionally useful acmes. This species is generally lumped into "*Z.erectus*" in palaeoceanographical studies, and is thus the principal supposed "high fertility index". It is easily distinguished from *Z.erectus*, however, by its smaller size (2-3µm long), compact form (with very small central openings) and overall low birefringence (mid-grey). A larger (4-5µm long), more elongate variety seems restricted to the uppermost Hauterivian - this form was noted in both Core 7B and Borehole 81/43 but only recorded separately in the latter section. This larger variety is, however, associated with a major *Z.noeliae* acme, and the two forms are likely conspecific.

Zeugrhabdotus scutula (Bergen, 1994) comb. nov.

Plate 10, Figs. 10-15 (EM & LM);
Plate 11, Figs. 11-13 (LM).

1989 *Zeugrhabdotus sisyphus* (Gartner, 1968) Crux, p.198, pl.8.7, fig.1 (EM); pl.8.12, fig.30 (LM).
1994 *Reinhardites scutula* Bergen, p.64, pl.1, figs.24-25 (EM & LM; same specimen).

Description - This species is characteristically medium-large (6-9µm long), with wide central openings. The relatively narrow wall is bicyclic, but the inner, proximal cycle is rudimentary; this inner cycle is barely visible on the LM, except along the minor axis of the coccolith where it is thickened to form triangular supports for the bridge. These four triangular projections, which support the two (distally fused) bars of the bridge are conspicuous on the LM (see Plate 10, Fig. 15), especially in specimens in which the bridge has broken out . The fairly narrow bridge consists of two optically separate bars that are fused and surmounted by a diamond-shaped distal process. The whole coccolith is moderately birefringent (grey-white), with the distal process yielding the brightest birefringence.
Remarks - Previous authors have assigned this species to *Z.sisyphus*, but included several other species (e.g. *Z.trivectis*) in this category, giving a much longer, composite range. Gartner (1968, p.34) noted that his Upper Cretaceous *Z.sisyphus* contained "a hopeless variety of forms", but most of the forms he illustrated are more thickly constructed than these Lower Cretaceous forms, and are probably more akin to *"Reinhardites" anthophorus* (Deflandre, 1959) Perch-Nielsen, 1968. Bergen (1994) reports that *Z.scutula* gives rise to *R.anthophorus* in the Upper Cretaceous. Thus *Z.sisyphus* is too ill-defined to be useful, and is probably best abandoned.

Occurrence - This species first appears in the Upper Hauterivian *speetonensis* ammonite Zone of Speeton, Borehole 81/43, and Germany, and in the corresponding *sayni* ammonite Zone of Tethys (Bergen, 1994). It is thus an important inter-regional marker.

Zeugrhabdotus sp. cf. *Z.scutula*

Remarks - This is the likely precursor of the relatively large and conspicuous *Z.scutula*. It is distinguished from this descendant by its smaller size (<6μm long), more delicate form, and by the absence of clear triangular bridge supports. It is distinguished from all other contemporary zeugrhabdotids by its delicate form - both the wall and bridge are much more delicate than in other species, and the wall appears unicyclic on the LM. The bridge bears a narrow spine base, unlike *Z.diplogrammus*. The whole coccolith is moderately birefringent (grey-white).

Zeugrhabdotus spiralis (Bramlette & Martini, 1964) nov.comb.

1964 *Zygodiscus spiralis* Bramlette & Martini, p.303, pl.4, figs.6-8 (LM).
1976 *Zygodiscus spiralis* Bramlette & Martini, 1964; Hill, pl.12, figs.28-37 (LM).

Remarks - This species has a wall that is clearly bicyclic throughout its height, and exhibits strong spiral extinction gyres. It is distinguished from other species with similarly constructed rims (most notably *Z.xenotus*) by the structure of its bridge, which is bisected by a narrow, diagonal extinction line (this probably reflects the mode of attachment of the distal process).

Zeugrhabdotus trivectis Bergen, 1994

Plate 11, Fig. 8 (LM).

Description - This distinctive, medium-sized (5-6μm long) species has a well-developed inner, proximal wall cycle. Thus, in cross-polarised light, the rim appears clearly bicyclic throughout its height, with equally well-developed inner and outer cycles; the inner cycle is brighter (white) than the outer (grey) and the extinction gyres are spirally arranged. The bridge, which arises from the inner wall cycle, consists of two fused bars and bears a relatively small, solid distal process.
Differentiation - This form is differentiated from other species of *Zeugrhabdotus* by its bicyclic rim extinction pattern and relatively simple bridge. The construction of its rim is most similar to *Zeugrhabdotus xenotus*, but this species has an X-shaped bridge and a prominent hollow spine.

Range - First appeared in the North Sea area during the Late Valanginian, becoming common in the Late Hauterivian.

Zeugrhabdotus xenotus (Stover, 1966) comb. nov.

Plate 11, Fig. 10 (LM).

1966 *Zygolithus xenotus* Stover, p.149, pl.4, figs.16-17 (LM); pl.9, fig.2.
1976 *Zygodiscus xenotus* (Stover, 1966) Hill, p.163, pl.12, figs.38-46 (LM); pl.15, fig.29 (EM).

Remarks - This is a distinctive species, amply described by Stover (1966), but ignored by most subsequent authors. The rim is constructed similarly to *Z.trivectis* and *Z.spiralis*, and is clearly bicyclic throughout its height, with spirally arranged extinction gyres; these species are differentiated by the structure of their bridges. In *Z.xenotus* the bars forming the bridge are bent to form a tight "X", with a prominent hollow spine rising from their juncture. The central "X" is best viewed with the axes of the coccolith oriented parallel to the polarisers; when oriented at 45° the bars appear parallel. The coccolith is moderately to strongly birefringent (grey to yellow), depending on its size.
Occurrence - This species first appears, in abundance, in the Aptian of the Heslerton Borehole, but was recorded very rarely and sporadically down to the Hauterivian in other sections. Bergen (1994) records the first occurrence of this species in the Early Valanginian of Tethys. Thus it seems to have been a predominantly Tethyan form, that did not successfully colonise the northern seaways until after the great transgressions of the Aptian.

Spicular Nannofossils (?Ascidian Spicules)

Remarks - Varol & Houghton (1993, and *in press*) recognise a number of types of fossil ascidian spicule and highlight the need for nannopalaeontologists to record such spicules. Ascidians (= sea squirts) are sessile, filter feeding tunicates, and important members of the benthos in modern shelf seas. Certain living ascidians secrete aragonitic spicules of distinctive morphology and comparable spicules are often encountered in nannofossil smear slides, but generally ignored, due their similarity to inorganic crystal precipitates. In the present study, such spicules were only systematically recorded in Borehole 81/43, having previously been regarded as inorganic precipitates. Nevertheless, a number of distinctive spicule types were recognised, and several are tentatively assigned to Cenozoic genera. It has been suggested that *Triquetrorhabdulus* and *Kokia* may be of ascidian origin (Varol & Girgis; 1994; Varol & Houghton, *in press*), but this is considered unlikely (see discussion under *Triquetrorhabdulus*). *Kokia* is formed from

flat, rather than spindle-shaped rays, and is probably related to *Micrantholithus* (van Niel, 1994).

Genus ***Micrascidites*** Deflandre & Deflandre-Rigaud, 1956

***Micrascidites?* sp.**

Plate 27, Figs. 1-4 (EM & LM).

Description - Elongate, spindle-shaped spicule (occasionally slightly trapezoidal) with two equally pointed ends. The maximum width is at mid-length. Length varies from 4-15μm, but the form of the spicules is remarkably consistent. These spicules are highly birefringent, unless oriented parallel to the polarisers, when they are optically extinct.
Occurrence - Extremely abundant in the Upper Kimmeridgian of Borehole 81/43; these spicules outnumber coccoliths by a ratio of 4:1 in one particular sample. These spicules are also observed in Tithonian material, but have not been recorded from the Cretaceous. This indicates a limited stratigraphical range.
Remarks - These spicules appear optically similar to the rays of *Micrascidites*, as illustrated by Varol & Houghton (*in press*), but the SEM reveals that they are solidly constructed, rather than fibrous. Recrysallisation from original aragonite to calcite may have resulted in this loss of structure. They are certainly calcareous - treatment with dilute hydrochloric acid resulted in complete dissolution of all spicules. The spicules occasionally form irregularly radiating groups, as in *Micrascidites*.

Genus ***Monniotia*** Varol & Houghton, *in press*

***Monniotia?* sp.**

Plate 27, Figs. 5-7 (EM & LM).

Description - Bundled aggregate of needle-like rays. The rays are thickened at one end, with the thick, parallel-sided ends fused to form a broad "base". The free parts of the rays are finely tapered. The whole structure is large (about 20μm long, with the "base" about 10μm wide) and highly birefringent. The bundles are observed in varying states of disaggregation, and individual rays are fairly common in some samples.
Occurrence - Hauterivian to Lower Barremian of Borehole 81/43, Speeton and Germany; rare through most of this interval but recorded fairly consistently in the uppermost Hauterivian of Borehole 81/43. This form was also recorded in the Upper Aptian of Germany, but this section yielded reworked Late Hauterivian coccoliths.

Remarks - These clusters differ from *Monniotia* in having a non-spherical habit - the spicules are arranged side-by-side, rather than radiating from a centre. The SEM reveals that individual rays are fibrous.

Spicule sp.1

Plate 27, Fig. 8 (LM).

Description - Elongate, lanceolate spicules that taper towards a fine point at one end; the other, blunt end may be either square, rounded or less finely pointed. Maximum width is at or close to the blunt end of the spicule. The ratio of length to maximum width is in the order of 4:1 to 8:1. These spicules are generally 12-15μm long, and highly birefringent when oriented obliquely to the polarisers.
Occurrence - Rare in the Hauterivian and Lower Barremian of Borehole 81/43; these spicules occur most consistently in the basal Barremian of this section. These spicules are also observed, much more commonly, in Tithonian material, so this would seem to be a long-ranging, conservative morphotype (or an inorganic precipitate?).

Spicule sp.2

Plate 27, Figs. 9 & 10 (LM).

Description - Nail-shaped spicules, in which the "nail head" is composed of three radiating knobs (one of which stands vertically). A long blade extends from this triradiate construction - this commonly flares away from the triradiate end (Plate 27, Fig. 9), but can also be pointed (Plate 27, Fig. 10). The whole structure is about 15μm long and highly birefringent, with the vertically standing knob reaching blue birefringence.
Occurrence - Rare in the Hauterivian of Borehole 81/43; only recorded with any regularity in the uppermost Hauterivian (above the range of *Tegulalithus septentrionalis*).

2.5 - PHOTOGRAPHIC PLATES

PLATE 1

PLATE 1

Scanning Electron Micrographs; scale bar at top of each micrograph = 1μm.

Figs. 1 & 4: ***Loxolithus armilla.***
Fig. 1, UCL Neg. 4079/13, Borehole 81/43, 14.70m, distal view.
Fig. 4, UCL Neg. 4079/12, same specimen (tilted).

Fig. 2: ***Staurolithites* sp..**
UCL Neg. 4062/12, Borehole 81/43, 46.53m, distal view.

Fig. 3: ***Chiastozygus* sp..**
(= *Chiastozygus platyrhetus?* - LM-SEM transfer required)
UCL Neg. 4063/8, Borehole 81/43, 41.16m, distal view.

Fig. 5: ***Staurolithites* sp..**
(= *Staurolithites crux* or *Staurolithites* sp.1? - LM-SEM transfer required)
UCL Neg. 4060/6, Borehole 81/43, 17.00m, distal view.

Fig. 6: ***Chiastozygus* sp..**
(= *Chiastozygus* sp.2? - LM-SEM transfer required)
UCL Neg. 4070/12, Borehole 81/43, 29.37m, distal view (note curvature of the X-bars).

Figs. 7-9: ***Staurolithites mutterlosei.***
Fig. 7, UCL Neg. 4068/27, Borehole 81/43, 18.00m, distal view.
Fig. 8, UCL Neg. 4068/35, Borehole 81/43, 18.00m, distal view.
Fig. 9, UCL Neg. 4068/37, Borehole 81/43, 18.00m, oblique distal view.

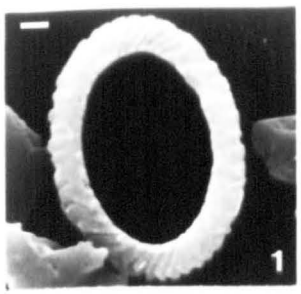
Fig. 10: ***Diadorhombus rectus.***
UCL Neg. 4067/27, Borehole 81/43, 31.76m, distal view.

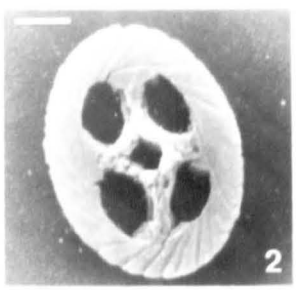
Fig. 11: ***Bukrylithus ambiguus.***
UCL Neg. 4076/27, Borehole 81/43, 41.16m, distal view.

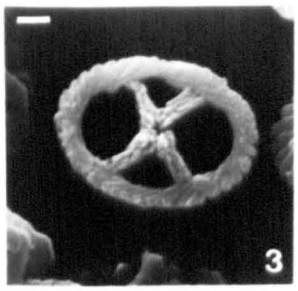
Fig. 12: ***?Diloma primitiva.***
UCL Neg. 4069/10, Borehole 81/43, 18.00m, distal view.

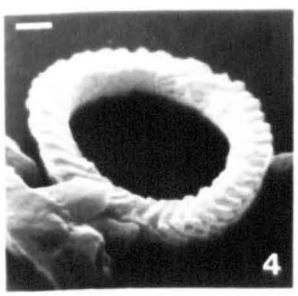
Figs. 13-15: ***Diloma galiciense.***
Fig. 13a, UCL Neg. 4074/11, Borehole 81/43, 17.00m, distal view.
Fig. 13b, UCL Neg. 4074/12, same specimen (tilted).
Fig. 14a, UCL Neg. 4074/26, Borehole 81/43, 17.00m, distal view.
Fig. 14b, UCL Neg. 4074/27, close-up of same specimen (tilted).
Fig. 15a, UCL Neg. 4074/24, Borehole 81/43, 17.00m, distal view.
Fig. 15b, UCL Neg. 4074/25, same specimen (tilted).

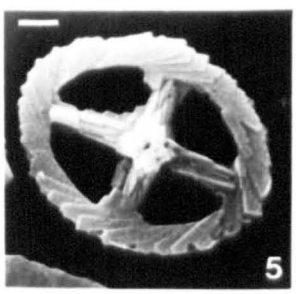
Plate 1

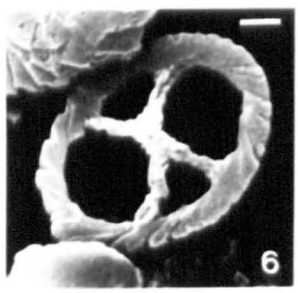

1

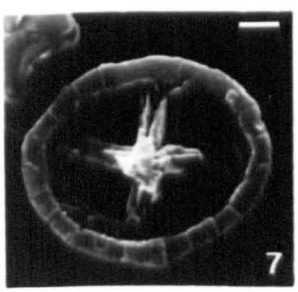

2

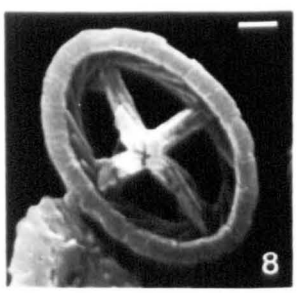

3

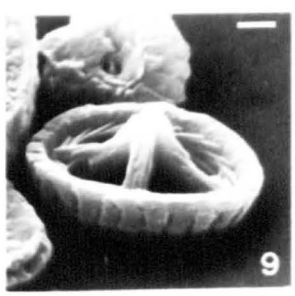

4

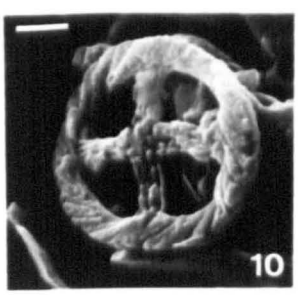

5

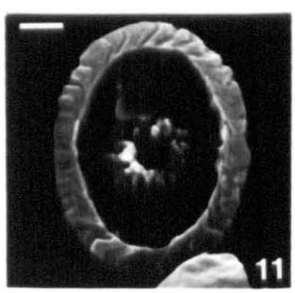

6

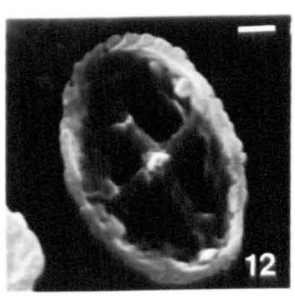

7

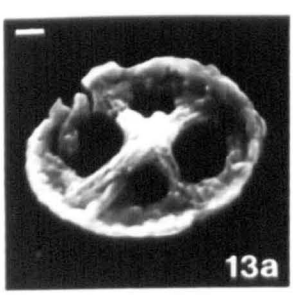

8

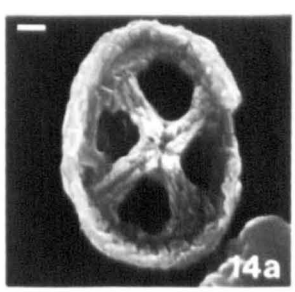

9

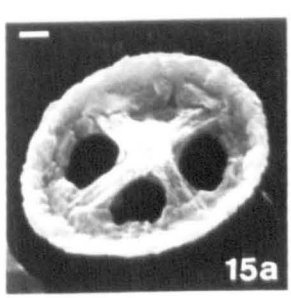

10

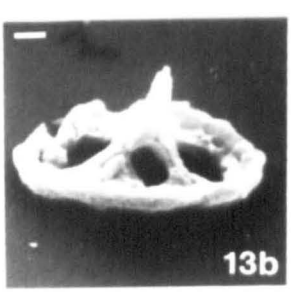

11

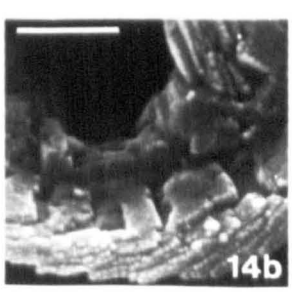

12


13a


14a


15a


13b


14b

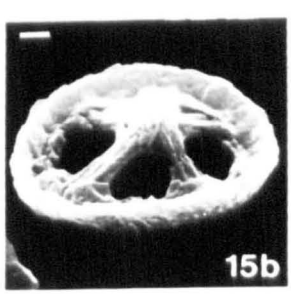

15b

PLATE 2

PLATE 2

Light Micrographs; all at 2000x magnification (scale bar in Fig.5 = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Fig. 1: ***Loxolithus armilla.*** UCL Neg. 5012/7, Speeton, Bed C2C (17); XP.

Fig. 2: ***Diadorhombus rectus.*** UCL Neg. 4020/34, Speeton, Bed C4C; XP.

Fig. 3: ***Staurolithites crux.*** UCL Neg. 3507/22, Speeton, Bed C2C (19); XP.

Fig. 4: ***Staurolithites* sp.1.** UCL Neg. 4099/14, Borehole 81/43, 28.77m; XP.

Figs. 5 & 8: ***Staurolithites mitcheneri.*** Fig.5, UCL Neg. 3507/1, Speeton, Bed C2B (13); XP. Fig.8, UCL Neg. 3722/20, Speeton, Bed LB4D (upper); XP.

Figs. 6-7: ***Staurolithites mutterlosei.*** Fig.6a, UCL Neg. 4095/8, Borehole 81/43, 34.47m; XP. Fig.6b, UCL Neg. 4095/9; XP, same specimen rotated 45°. Fig.6c, UCL Neg. 4095/10; same specimen in Ph. Fig.7, UCL Neg. 3722/16, Speeton, Bed LB4C; XP.

Fig. 9: ***Staurolithites dibrachiatus.*** Fig.9a, UCL Neg. 4071/26, Speeton, Bed C9C; XP. Fig.9b, UCL Neg. 4071/27; XP, same specimen rotated 45°. Fig.9c, UCL Neg. 4071/28; same specimen in Ph.

Fig. 10: ***Bukrylithus ambiguus.*** UCL Neg. 4097/21, Speeton, Bed LB5C.III; XP.

Fig. 11: ***Rhabdophidites parallelus.*** UCL Neg. 3513/5, Speeton, Bed C2B (16); XP.

Figs. 12-13: ***Diloma primitiva.*** Fig.12a, UCL Neg. 4020/28, Speeton, Bed C9C; XP. Fig.12b, UCL Neg. 4020/30; same specimen in Ph; note the arcuate bars (detached from the rim) forming the proximal plate. Fig.13, UCL Neg. 4722/1, Speeton, Bed LB3B; XP; oblate variety, with proximal plate appressed to the inner wall cycle.

Fig. 14 (a & b): ***Diloma galiciense.*** Fig.14a, UCL Neg. 4065/7, Borehole 81/43, 18.00m; XP. Fig.14b, UCL Neg. 4065/9; same specimen in Ph.

Fig. 15 (a & b): ***Staurolithites? glabra.*** Fig.15a, UCL Neg. 4089/18, Gault Clay (Folkestone), Bed VII (upper); XP; the outer, weakly birefingent cycle is a vertically standing marginal wall - the wall-like nature of this cycle becomes apparent on focusing through the specimen. Fig.15b, UCL Neg. 4089/20; same specimen in Ph; note outer wall (dark band).

Fig. 16 (a & b): ***Acaenolithus?* sp.1 (="*V.matalosa*" of Crux & Mutterlose).** Fig.16a, UCL Neg. 5005/15, Gott, *germanica* Zone; XP; appears very similar to *Staurolithites? glabra* in 2 dimensions, but has several superimposed shields, and lacks the marginal wall of *S? glabra.* Fig.16b, UCL Neg. 5005/16; same specimen in Ph; note absence of marginal wall.

Fig. 17 (a & b): ***Acaenolithus?* sp.2.** Fig. 17a, UCL Neg. 5005/13, Atherfield Clay, AC 2; XP. Fig.17b, UCL Neg. 5005/14; same specimen in Ph.

Fig. 18 (a & b): ***Acaenolithus ?galloisii.*** Fig.18a, UCL Neg. 5005/11, Heslerton Borehole, BH-2 (86); XP; a long-ranging form, transitional with the Upper Cretaceous *Broinsonia signata* (these forms are inseparable on the LM). Fig.18b, UCL Neg. 5005/12; same specimen in Ph.

Fig. 19 (a & b): ***Acaenolithus viriosus.*** Fig.19a, UCL Neg. 4074/27, Heslerton Borehole, BH-2 (85); XP. Fig.19b, UCL Neg. 4074/28; XP, same specimen rotated 45°.

Fig. 20 (a & b): ***Gartnerago nanum.*** Fig.20a, UCL Neg. 4095/28, Heslerton Borehole, CS-14; XP. Fig.20b, UCL Neg. 4095/29; same specimen in Ph.

Fig. 21 (a & b): ***Gartnerago theta.*** Fig.21a, UCL Neg. 4095/25, Heslerton Borehole, CS-14; XP. Fig.21b, UCL Neg.4095/26; same specimen in Ph.

Fig. 22: ***Conusphaera rothii.*** UCL Neg. 4099/21, Borehole 81/43, 28.77m; XP.

Plate 2

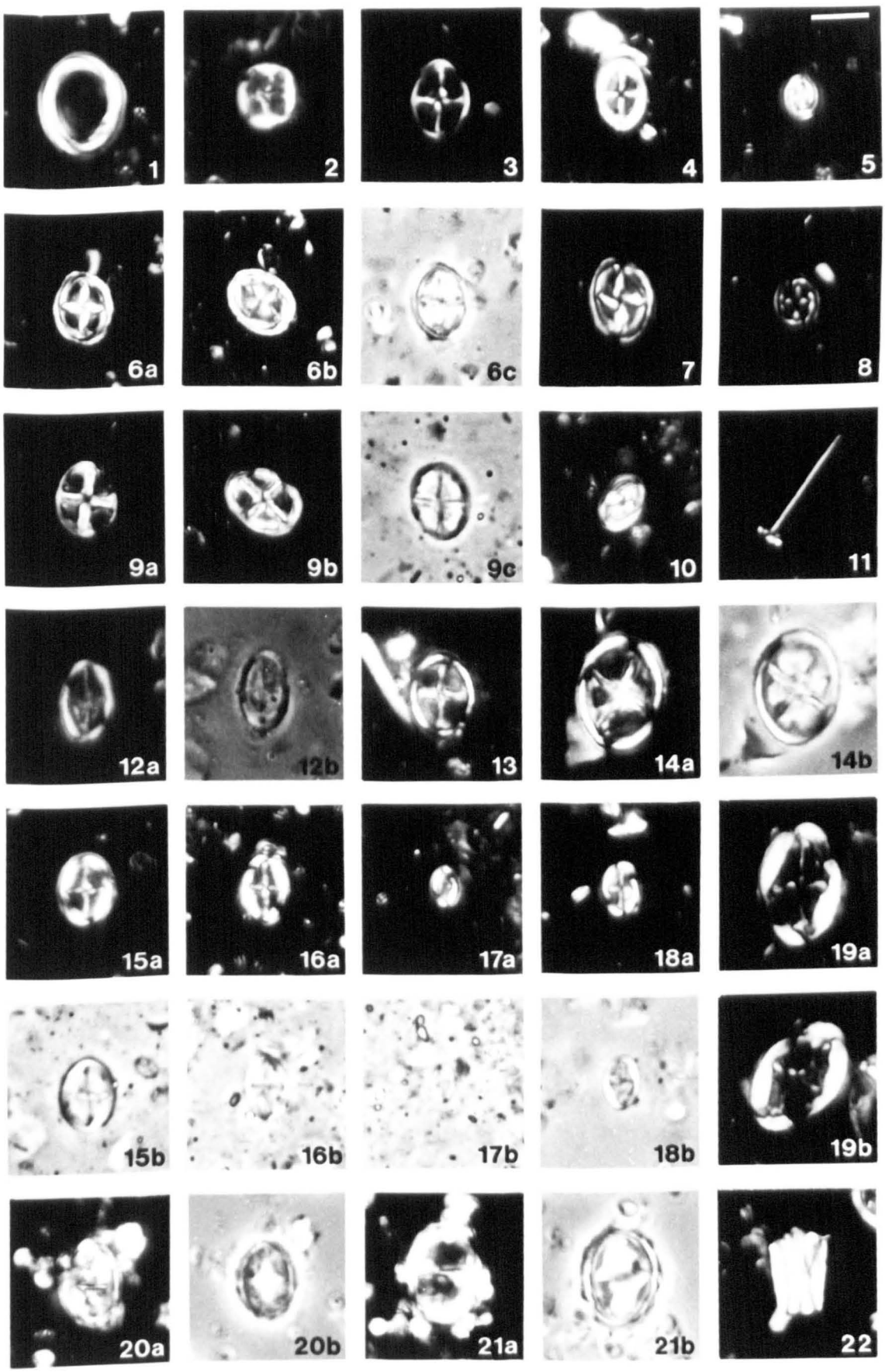

1
2
3
4
5
6a
6b
6c
7
8
9a
9b
9c
10
11
12a
12b
13
14a
14b
15a
16a
17a
18a
19a
15b
16b
17b
18b
19b
20a
20b
21a
21b
22

PLATE 3

PLATE 3

Scanning Electron Micrographs; scale bar at the top of each micrograph = 1μm.

Figs. 1-6: ***Eiffellithus striatus.***
Fig.1, UCL Neg. 4062/5, Borehole 81/43, 46.53m; distal view.
Fig.2, UCL Neg. 4061/27, Borehole 81/43, 46.53m; distal view.
Fig.3, UCL Neg. 4068/4, Borehole 81/43, 62.38m; distal view (plate-formed inner cycle arrowed).
Fig.4 , UCL Neg. 4062/18, Borehole 81/43, 46.53m; distal view (tilted).
Fig.5, UCL Neg. 4062/7, Borehole 81/43, 46.53m; oblique proximal view.
Fig.6, UCL Neg. 4061/33, Borehole 81/43, 46.53m; proximal view (proximal wall cycle arrowed).

Fig. 7: ***Eiffellithus windii.***
UCL Neg. 4073/13, Borehole 81/43, 64.79m; distal view (overgrown specimen).

Fig. 8-9: ***Eiffellithus turriseiffelii.***
Fig.8, UCL Neg.?, Cenomanian, England; distal view (overgrown specimen).
Fig.9, UCL Neg.?, Cenomanian, England; distal view.

Fig. 10-12: ***Tegumentum bergeni*** **(sp. nov.).**
Fig.10a, UCL Neg. 4067/16, Borehole 81/43, 31.76m; distal view, **isotype.**
Fig.10b, UCL Neg. 4067/17; same specimen (tilted).
Fig.11a, UCL Neg. 4069/8, Borehole 81/43, 18.00m; distal view.
Fig.11b, UCL Neg. 4069/9; same specimen (tilted).
Fig.12, UCL Neg. 4067/23, Borehole 81/43, 31.76m; distal view.

Fig. 13: ***Tegumentum octiformis.***
UCL Neg. 4067/19, Borehole 81/43, 31.76m; distal view.

Plate 3

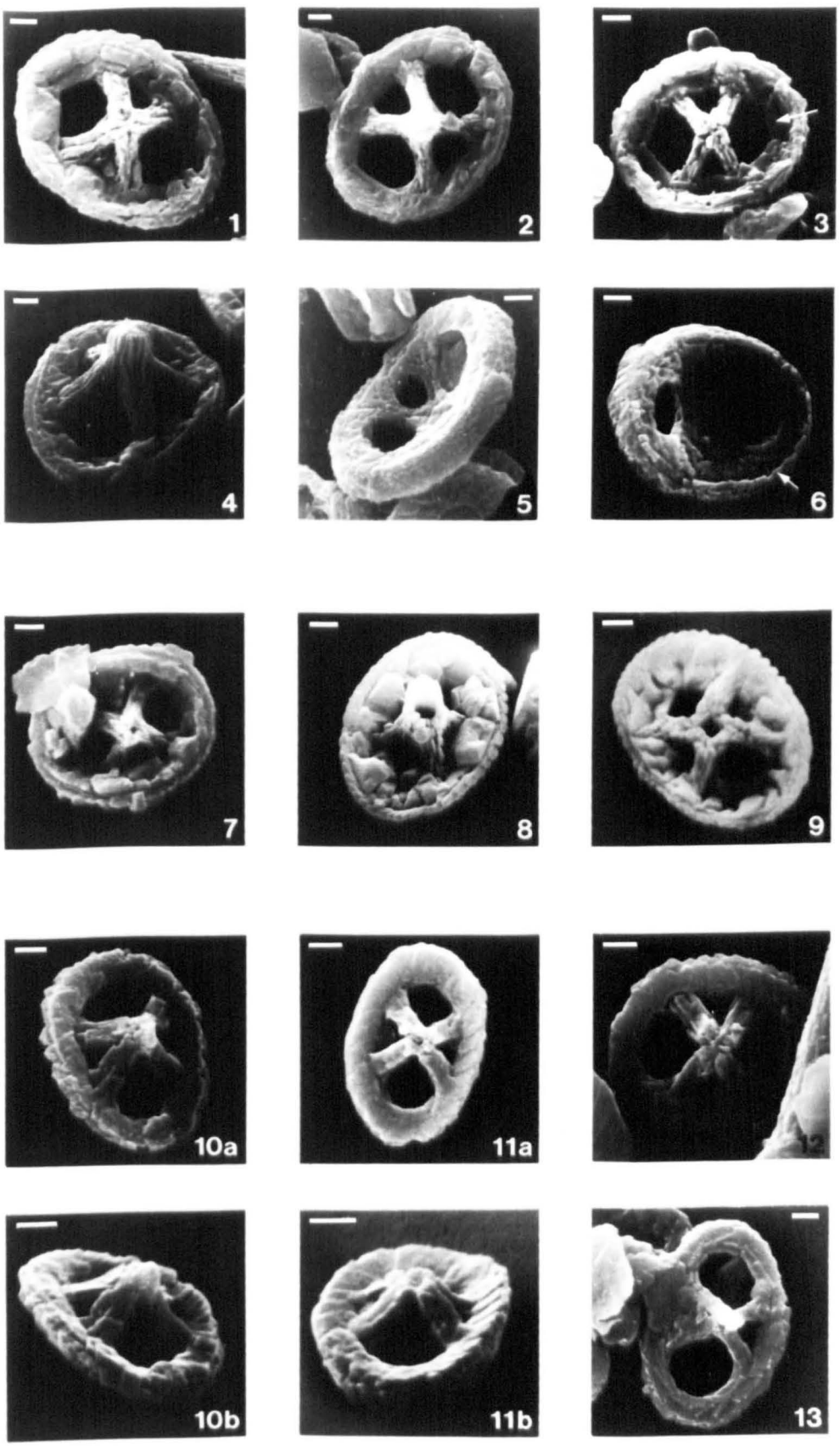


PLATE 4

PLATE 4

Light Micrographs; all at 2000x magnification (scale bar in Fig.2c = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Figs. 1-2: ***Eiffellithus windii.*** Fig.1a, UCL Neg. 4099/29, spot sample from the middle Valanginian (dated here) of Tunisia; XP. Fig.1b, UCL Neg. 4099/30; same specimen rotated 45°. Fig.2a, UCL Neg. 4097/12; Borehole 81/43, 65.33m; Ph. Fig.2b, UCL Neg. 4097/9; same specimen in XP. Fig.2c, UCL Neg. 4097/11; XP, same specimen rotated 45°.

Fig. 3 (a-c): ***Eiffellithus striatus.*** Fig.3a, UCL Neg. 4097/4, Speeton, Bed C7E; XP. Fig.3b, UCL Neg. 4097/5; XP, same specimen rotated 45°. Fig.3c, UCL Neg. 4097/6; same specimen in Ph.

Fig. 4 (a & b): ***Eiffellithus turriseiffelii.*** Fig.4a, UCL Neg. 4099/28, Gault Clay (Folkestone), Bed XIII (base); Ph. Fig.4b, UCL Neg. 4099/27; same specimen in XP.

Figs. 5-6 & 9: ***Tegumentum bergeni* var. *bergeni.*** (Fig.5 = typical size; Figs.6 & 9 = larger specimens) Fig.5a, UCL Neg. 4097/33, Borehole 81/43, 12.79m; XP. Fig.5b, UCL Neg. 4097/34; XP, same specimen rotated 45°. Fig.5c, UCL Neg. 4097/35; same specimen in Ph. Fig.6a, UCL Neg. 4065/19, Borehole 81/43, 18.00m; Ph. Fig.6b, UCL Neg. 4065/18; same specimen in XP. Fig.9, UCL Neg. 4094/5, Gault Clay (Folkestone), Bed VII (upper); XP; large, late form with clearly recurved X-bars.

Fig. 7 (a-c): ***Tegumentum bergeni* var. *minor.*** Fig.7a, UCL Neg. 4099/8, Speeton, Bed LB5C.III; XP. Fig.7b, UCL Neg. 4099/9; XP, same specimen rotated 45°. Fig.7c, UCL Neg. 4099/10; same specimen in Ph.

Fig. 10: ***Tegumentum bergeni* var. *quasioctiformis.*** Fig.10a, UCL Neg. 4097/16, Speeton, Bed LB5C.III; XP. Fig.10b, UCL Neg. 4097/17; XP, same specimen rotated 45°. Fig.10c, UCL Neg. 4097/18; same specimen in Ph.

Fig. 8 & 11: ***Tegumentum octiformis.*** Fig.8, UCL Neg. 5005/29, Borehole 81/43, 11.92m; XP. Fig.11a, UCL Neg. 5012/30, Borehole 81/43, 24.90m; Ph. Fig.11b, UCL Neg. 5012/31, same specimen in XP.

Fig. 12 (a & b): ***Chiastozygus* sp.1.** Fig.12a, UCL Neg. 5005/21, Borehole 81/43, 63.60m; XP. Fig.12b, UCL Neg. 5005/22; same specimen in Ph.

Fig. 13 (a-c): ***Chiastozygus* sp.2.** Fig.13a, UCL Neg. 4023/29, Borehole 81/43, 41.16m; XP. Fig.13b, UCL Neg. 4023/28; same specimen rotated 45°. Fig.13c, UCL Neg. 4023/30; same specimen in Ph.

Fig. 14 (a-c): ***Chiastozygus* sp.3 (= *C.platyrhetus?*).** Fig.14a, UCL Neg. 4097/13, Borehole 81/43, 12.79m; XP. Fig.14b, UCL Neg. 4097/14; XP, same specimen rotated 45°. Fig.14c, UCL Neg. 4097/15; same specimen in Ph.

Fig. 15 (a & b): ***Chiastozygus* sp.4.** Fig.15a, UCL Neg. 3315/21, Gault Clay (Folkestone), Bed X; XP. Fig.15b, UCL Neg. 3315/22; same specimen in Ph; note relatively large size and robust form, relative to Neocomian forms of *Chiastozygus.*

Plate 4

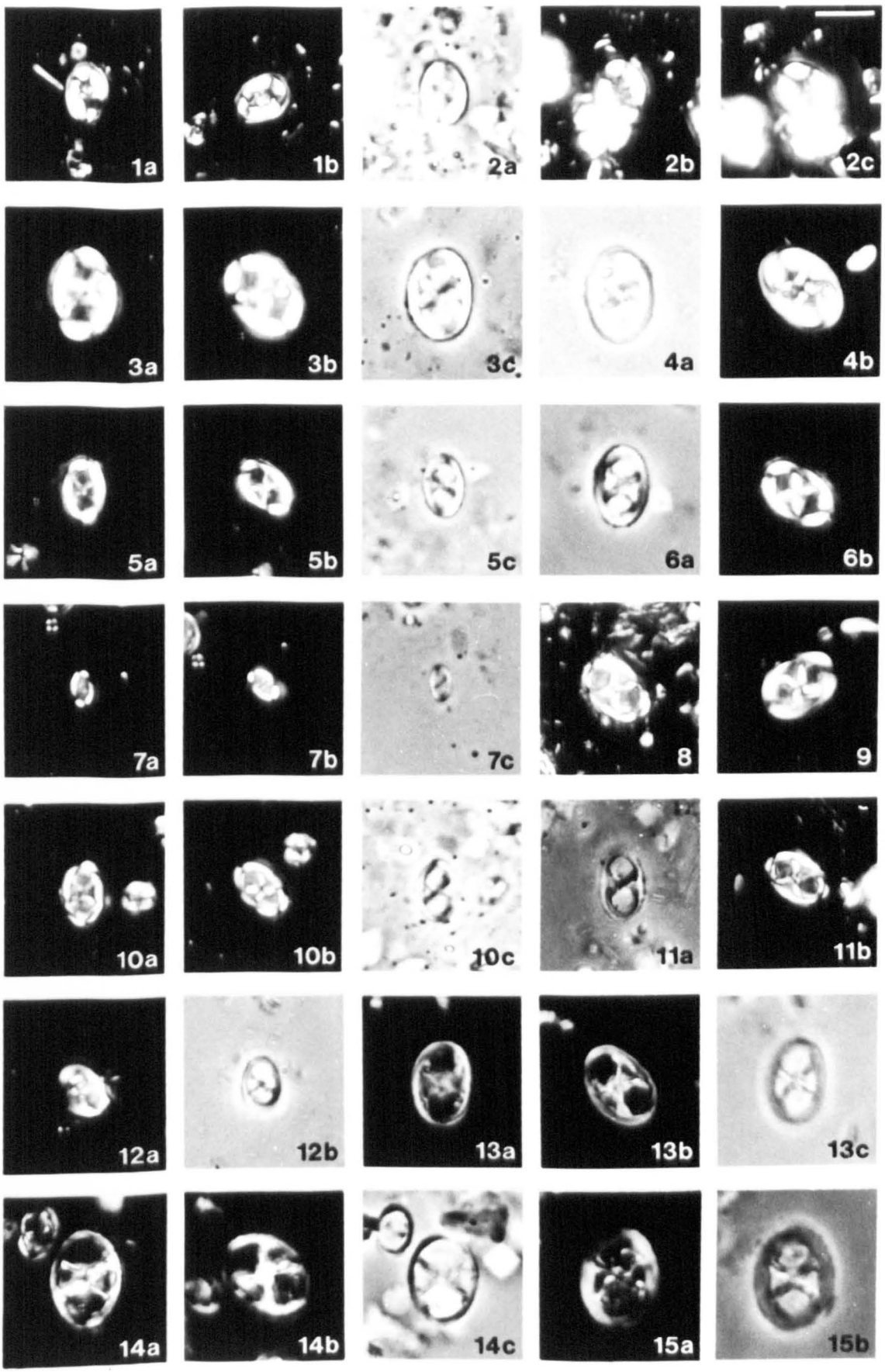

1a
1b
2a
2b
2c
3a
3b
3c
4a
4b
5a
5b
5c
6a
6b
7a
7b
7c
8
9
10a
10b
10c
11a
11b
12a
12b
13a
13b
13c
14a
14b
14c
15a
15b

PLATE 5

PLATE 5

Rhagodiscaceae

Scanning Electron Micrographs; scale bar at top of each micrograph = 1μm.

Figs. 1-6 : ***Rhagodiscus pseudoangustus.***
Fig.1, UCL Neg. 4068/14, Borehole 81/43, 18.00m, distal view.
Fig.2, UCL Neg. 4068/15, Borehole 81/43, 18.00m, distal view.
Fig.3, UCL Neg. 4068/12, Borehole 81/43, 18.00m, distal view.
Fig.4, UCL Neg. 4069/6, Borehole 81/43, 18.00m, oblique side view.
Fig.5, UCL Neg. 4068/15, same specimen as Fig. 2 (tilted).
Fig.6, UCL Neg. 4068/20, Borehole 81/43, 18.00m, proximal view.

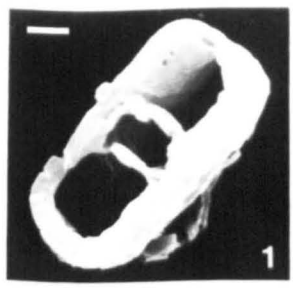
Fig. 7 (a-c): ***Rhagodiscus cepekii.***
Fig.7a, UCL Neg. 4068/34, Borehole 81/43, 18.00m, distal view (tilted).
Fig.7b, UCL Neg. 4068/32, same specimen.
Fig.7c, UCL Neg. 4068/33, same specimen.

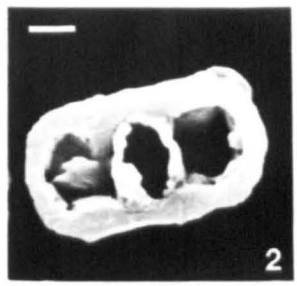
Figs. 8-9: ***Rhagodiscus infinitus.***
Fig.8a, UCL Neg. 4081/25, Borehole 81/43, 29.37m, distal view.
Fig.8b, UCL Neg. 4081/26, same specimen (tilted).
Fig.9, UCL Neg. 4081/27, Borehole 81/43, 29.37m, distal view.

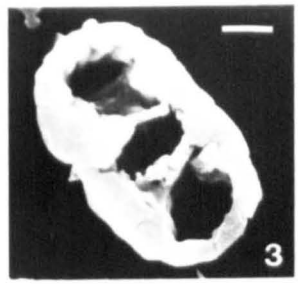
Figs. 10-13: ***Rhagodiscus asper.***
Fig.10a, UCL Neg. 4068/24, Borehole 81/43, 18.00m, distal view.
Fig.10b, UCL Neg. 4068/25, same specimen (tilted).
Fig.11, UCL Neg. 4074/1, Borehole 81/43, 32.80m, proximal view.
Fig.12, UCL Neg. 4060/4, Borehole 81/43, 17.00m, side view. Fig.13, UCL Neg. 3699/3, Speeton, Bed C2B (14), side view.

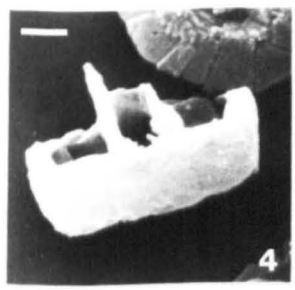
Fig. 14: ***Calcicalathina oblongata.***
UCL Neg. 4067/9, Speeton, Bed D1, distal view.

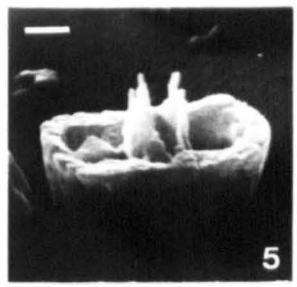
Plate 5

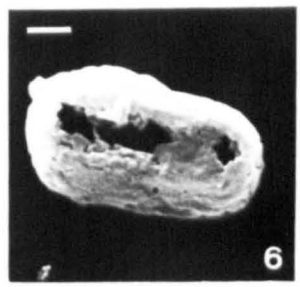

1

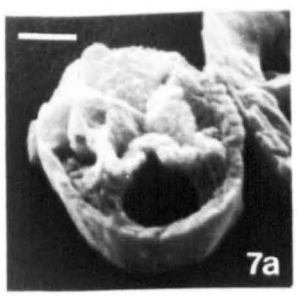

2

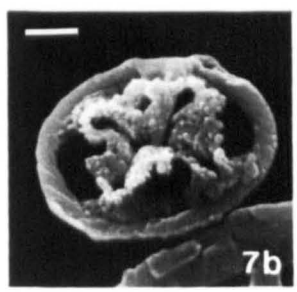

3

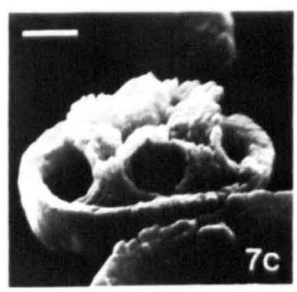

4

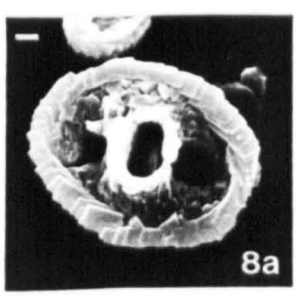

5

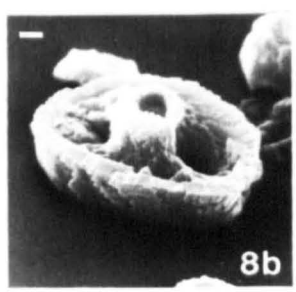

6

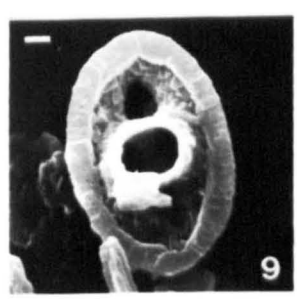

7a

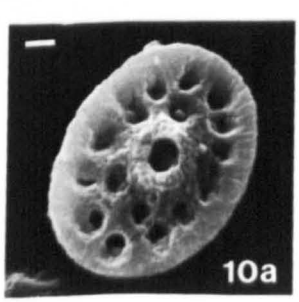

7b

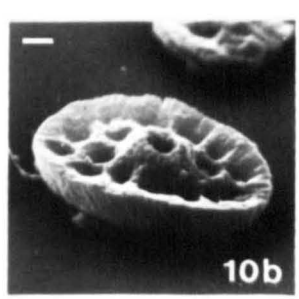

7c

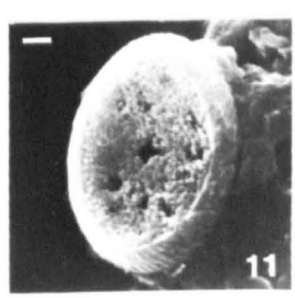

8a

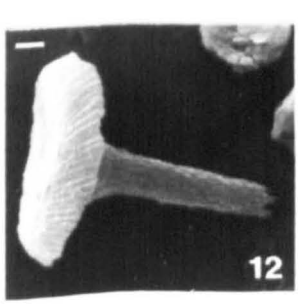

8b

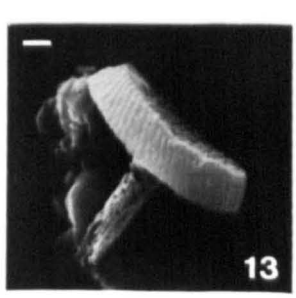

9


10a


10b


11


12


13

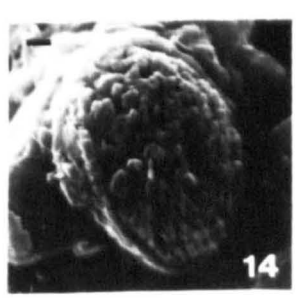

14

PLATE 6

PLATE 6

Light Micrographs; all at 2000x magnification (scale bar in Fig.3 = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Figs. 1 & 2: ***Perissocyclus plethotretus.*** Fig.1a, UCL Neg.4099/2, Borehole 81/43, 12.79m; XP. Fig.1b, UCL Neg. 4099/3; same specimen in Ph. Fig.2a, UCL Neg. 4023/9, Borehole 81/43, 41.16m; XP. Fig.2b, UCL Neg. 4023/10; same specimen in Ph.

Figs. 4 & 5: ***Perissocyclus tayloriae.*** Fig.4a, UCL Neg. 5015/1, Borehole 81/43, 45.01m; XP (note prominent distal process). Fig.4b, UCL Neg. 5015/2; same specimen in Ph. Fig.5a, UCL Neg. 5015/3, Borehole 81/43, 45.01m; XP. Fig.5b, UCL Neg. 5015/4; same specimen in Ph.

Figs. 3 & 6: ***Rhagodiscus asper.*** Fig.3, UCL Neg. 4024/33, Speeton, Bed C1B (4); XP. Fig.6, UCL Neg. 4074/6, Borehole 81/43, 29.37m; XP, collapsed coccosphere.

Fig. 7 (a & b): ***Calcicalathina oblongata.*** Fig.7a, UCL Neg. 4024/1, Speeton, Bed C8B (6); XP. Fig.7b, UCL Neg. 4024/2; XP, same specimen rotated 45°.

Fig. 8 (a & b): ***Rhagodiscus infinitus.*** Fig.8a, UCL Neg. 4024/5, Speeton, Bed C8B (1); XP. Fig.8b, UCL Neg. 4024/4; XP, same specimen rotated 45°.

Fig. 9: ***Rhagodiscus splendens.*** UCL Neg. 3315/3, Gault Clay (Folkestone), Bed X; XP.

Figs. 10-12: ***Rhagodiscus pseudoangustus.*** Fig.10, UCL Neg. 4065/5, Borehole 81/43, 18.00m; XP (var.1 - angular variety). Fig.11, UCL Neg. 4065/3, Borehole 81/43, 18.00m; XP, side view. Fig.12a, UCL Neg. 4065/21, Borehole 81/43, 18.00m; XP; A = more rounded variety of *R.pseudoangustus* (var.2); B = *Stradnerlithus hexserratus.* Fig.12b, UCL Neg. 4065/23; same specimens in Ph (B = *Stradnerlithus hexserratus*).

Figs. 14 & 15: ***Rhagodiscus angustus* subsp. *parvus.*** Fig.14, UCL Neg. 5015/8, Atherfield Clay, AC 13; XP. Fig.15, UCL Neg. 5015/9, Atherfield Clay, AC 13; XP.

Fig. 16 (a & b): ***Rhagodiscus angustus* subsp. *angustus.*** Fig.16a, UCL Neg. 4089/23, Gault Clay (Folkestone), Bed VII (upper); XP. Fig.16b, UCL Neg. 4089/24; same specimen in Ph.

Figs. 13 & 17: ***Rhagodiscus achlyostaurion.*** Fig.13, UCL Neg. 4089/27, Gault Clay (Folkestone), Bed VII (upper); XP. Fig.17, UCL Neg. 4089/28; same specimen in Ph.

Fig. 18: ***Lapideacassis glans.*** UCL Neg. 4020/5, Borehole 81/43, 13.70m; XP.

Figs. 19 & 20: ***Lapideacassis mariae.*** Fig.19, UCL Neg. 4024/20, Speeton, Bed LB3B; XP. Fig.20, UCL Neg. 4094/9, Heslerton Borehole, BH-2(66); XP.

Fig. 21 (a & b): ***Markalius?* sp. (?or protococcolith of *W.barnesae*).** Fig.21a, UCL Neg. 5012/14, Borehole 81/43, 13.70m; XP. Fig.21b, UCL Neg. 5012/15; same specimen in Ph.

Figs. 22-24: ***Lithraphidites moray-firthensis.*** Fig.22, UCL Neg. 4074/12, Heslerton Borehole, BH-2(67); XP. Fig.23a, UCL Neg. 4074/18, Heslerton Borehole, BH-2(67); XP. Fig.23b, UCL Neg. 4074/19; same specimen in Ph. Fig.24a, UCL Neg. 4074/22, Heslerton Borehole, BH-2(67); XP. Fig.24b, UCL Neg. 4074/23; same specimen in Ph.

Plate 6

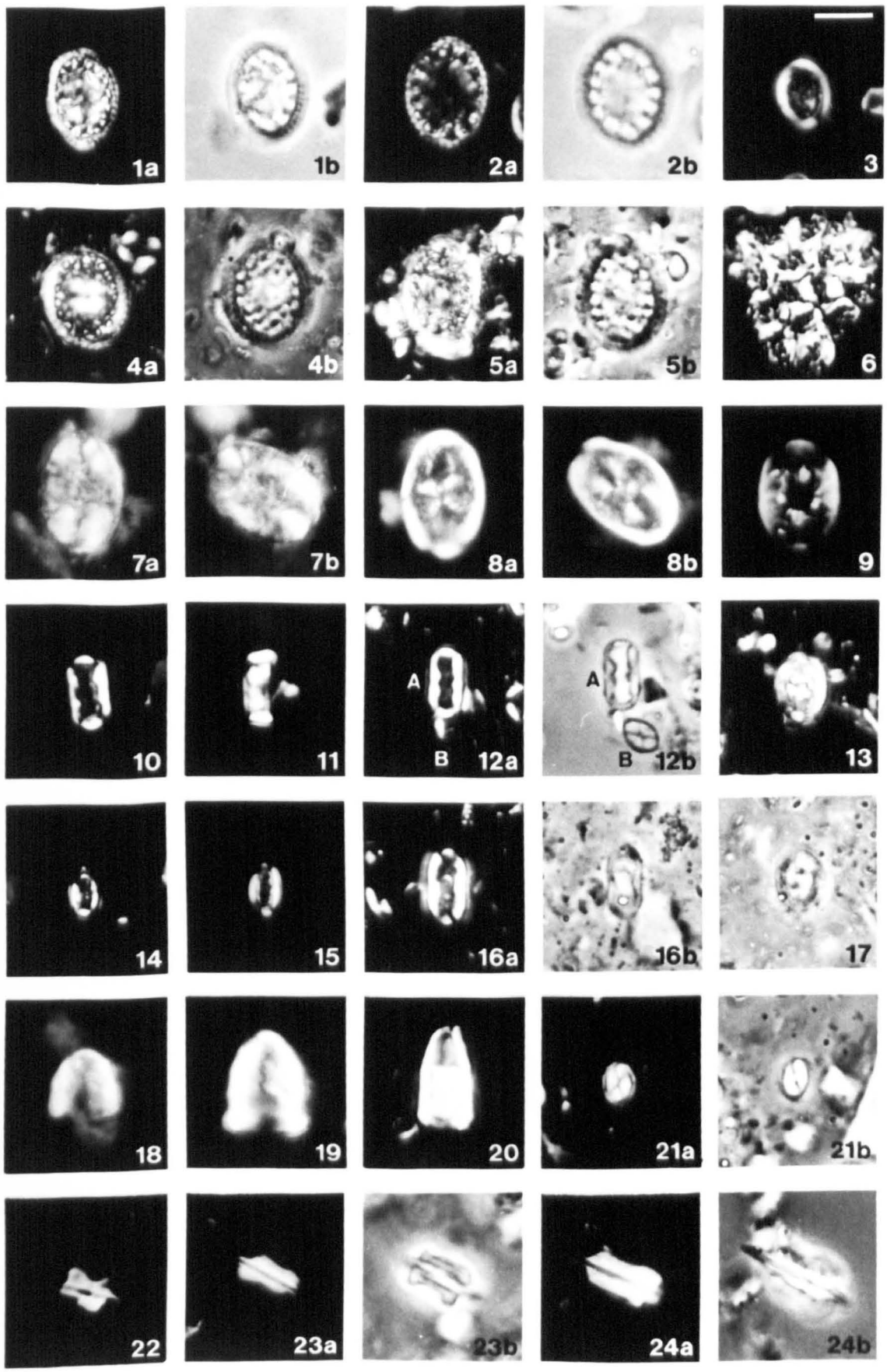

1a
1b
2a
2b
3
4a
4b
5a
5b
6
7a
7b
8a
8b
9
10
11
A
B
12a
A
B
12b
13
14
15
16a
16b
17
18
19
20
21a
21b
22
23a
23b
24a
24b

PLATE 7

PLATE 7

***Neoparhabdolithus* (gen. nov.)**

Figs. 1-7: ***Neoparhabdolithus stubbingsii.***

SEMs:
(scale bar at top of each micrograph = 1μm)

Fig.1a, UCL Neg. 4076/20, Borehole 81/43, 41.16m, side view.
Fig.1b, UCL Neg. 4076/18, oblique proximal view of same specimen.
Fig.1c, UCL Neg. 4076/19, close-up of proximal face.

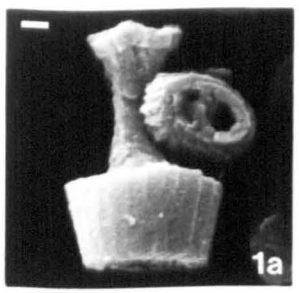
Fig.2, UCL Neg. 4060/28, Borehole 81/43, 41.16m, oblique distal view.
Fig.3, UCL Neg. 4076/12, Borehole 81/43, 41.16m, oblique proximal view.
Fig.4, UCL Neg. 4070/19, Borehole 81/43, 41.16m, oblique proximal view (etched specimen).

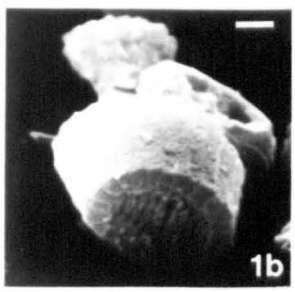
LMs:
(all to same magnification; scale bar in Fig.7a = 5μm)

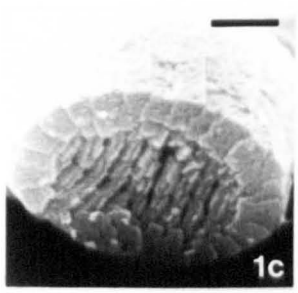
Fig.5, UCL Neg. 4023/18, Borehole 81/43, 41.16m; XP.
Fig.6, UCL Neg. 4023/8, Borehole 81/43, 41.16m; Ph.
Fig.7a, UCL Neg. 4023/14, Borehole 81/43, 41.16m; XP.
Fig.7b, UCL Neg. 4023/15; same specimen in Ph.

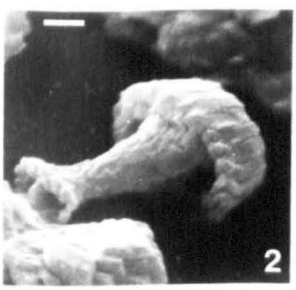
Figs. 8-9: ***Neoparhabdolithus* sp.1.**
(SEMs)
Fig.8a, UCL Neg. 4062/13, Borehole 81/43, 46.53m, side view.
Fig.8b, UCL Neg. 4062/14, proximal view of same specimen.
Fig.9, UCL Neg. 4063/2, Borehole 81/43, 11.92m, side view (overgrown specimen).

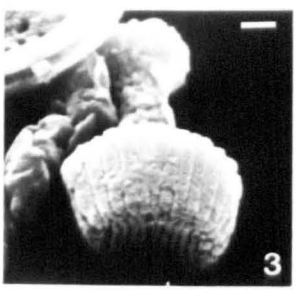
Plate 7

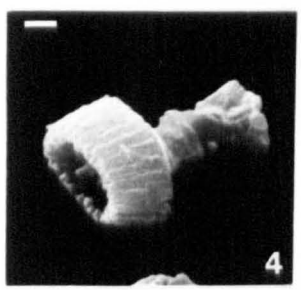

1a

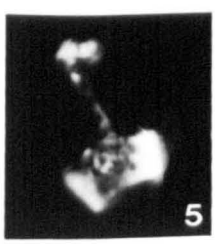

1b

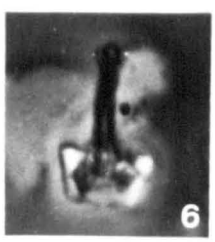

1c

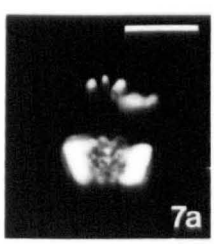

2

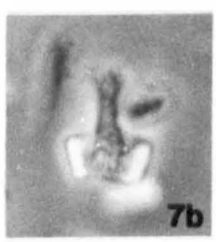

3

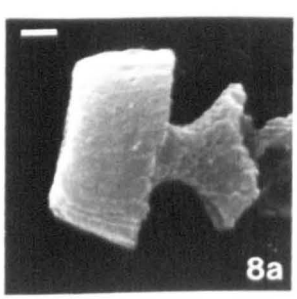

4

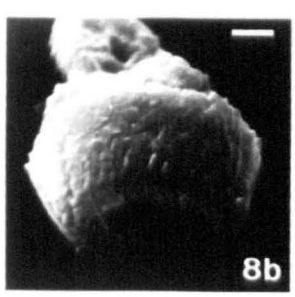

5


6


7a


7b


8a


8b

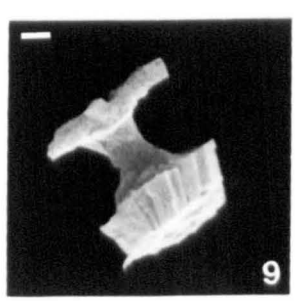

9

PLATE 8

PLATE 8

Scanning Electron Micrographs; scale bar at the top of each micrograph = 1μm.

Fig. 1: ***Stradnerlithus rhombicus.***
UCL Neg. 4079/31, Borehole 81/43, 7.12m, proximal view.

Figs. 2, 4 & 5: ***Clepsilithus maculosus*** **(sp. nov.).**
Fig.2a, UCL Neg. 4061/11, Borehole 81/43, 32.80m, distal view, **holotype.**
Fig.2b, UCL Neg. 4061/12, same specimen (tilted).
Fig.4, UCL Neg. 4074/7, Borehole 81/43, 32.80m, distal view.
Fig.5, UCL Neg. 4074/2, Borehole 81/43, 32.80m, distal view, **isotype.**

Fig. 3: ***Stradnerlithus silvaradius.***
UCL Neg. 4073/22, Borehole 81/43, 64.79m, distal view.

Figs. 6 & 8: ***Stradnerlithus hexserratus.***
Fig.6, UCL Neg. 4070/9, Borehole 81/43, 64.79m, distal view.
Fig.8, UCL Neg. 4073/18, Borehole 81/43, 64.79m, proximal view.

Figs. 7, 9 & 10: ***Rotelapillus laffittei.***
Fig.7a, UCL Neg. 4062/10, Borehole 81/43, 46.53m, distal view.
Fig.7b, UCL Neg. 4062/11, same specimen (tilted).
Fig.9, UCL Neg. 4061/14, Borehole 81/43, 32.80m, proximal view.
Fig.10, UCL Neg. 4061/22, Borehole 81/43, 32.80m, side view (broken specimen).

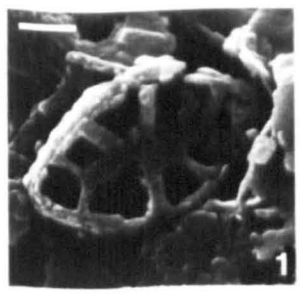
Figs. 11-14: ***Calculites burnettiae*** **(sp. nov.).**

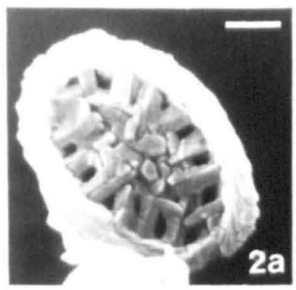
Fig.11: ***Calculites burnettiae*** **var.A.**
Fig.11a, UCL Neg. 4062/8, Borehole 81/43, 46.53m, ?distal view.
Fig.11b, UCL Neg. 4062/9, same specimen (tilted).

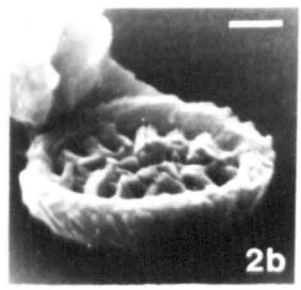
Fig. 12: ***Calculites burnettiae*** (transitional between var.A & var.B).
Fig.12a, UCL Neg. 4061/30, Borehole 81/43, 46.53m, ?proximal view.
Fig.12b, UCL Neg. 4061/29, same specimen (tilted).

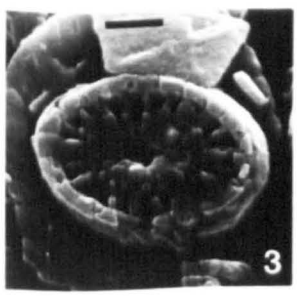
Figs.13 & 14: ***Calculites burnettiae*** **var.B.**
Fig.13, UCL Neg. 4061/32, Borehole 81/43, 46.53m.
Fig. 14, UCL Neg. 4076/30, Borehole 81/43, 46.53m.

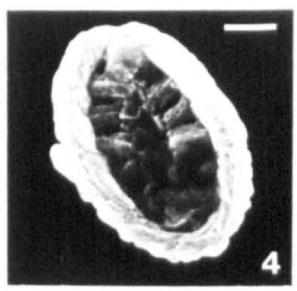
Plate 8

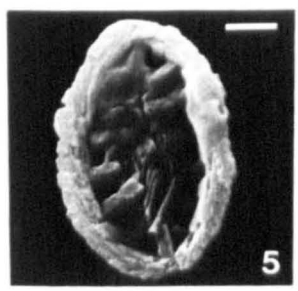

1

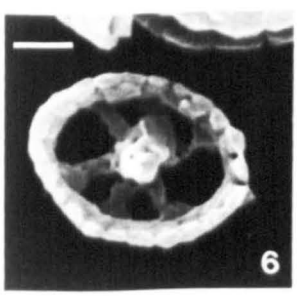

2a

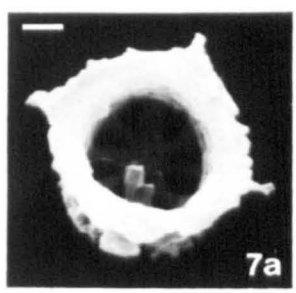

2b

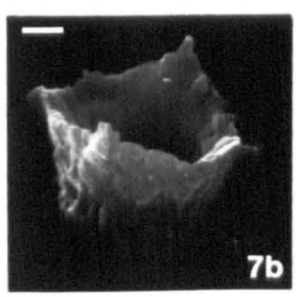

3

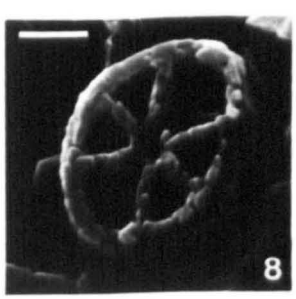

4

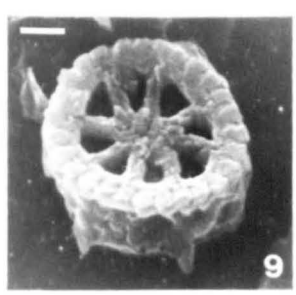

5

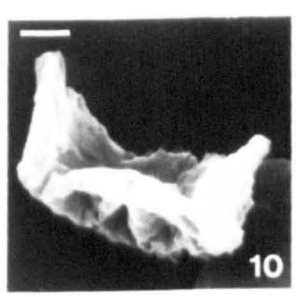

6

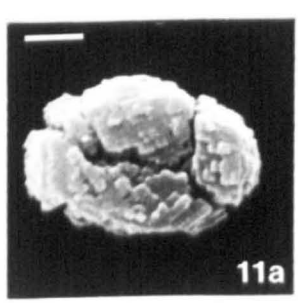

7a

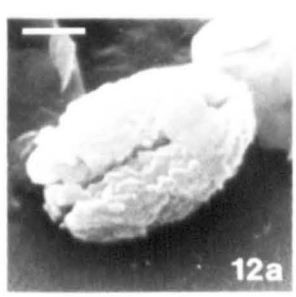

7b

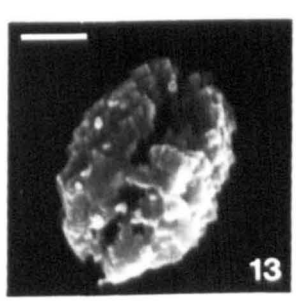

8

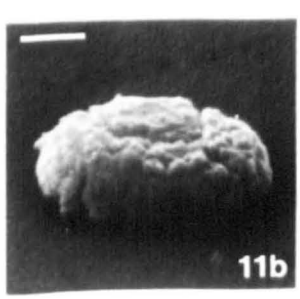

9

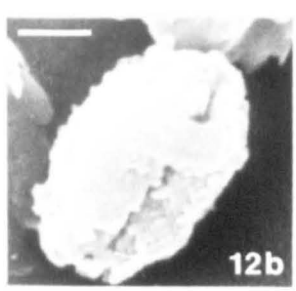

10


11a


12a


13


11b


12b

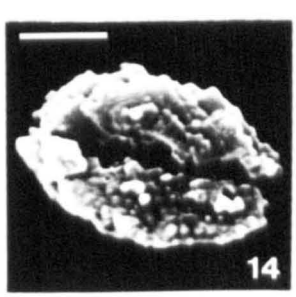

14

PLATE 9

PLATE 9

Light Micrographs; all at 2000x magnification (scale bar in Fig.5a = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Fig. 1 (a & b): ***Calculites?* sp.1.** Fig.1a, UCL Neg. 3697/7, Speeton, Bed D1; XP. Fig.1b, UCL Neg. 3697/8; XP, same specimen rotated 45°.

Fig. 2-5: ***Calculites burnettiae* (sp. nov.).**

Figs.2 & 3: ***Calculites burnettiae* var.A.** Fig.2a, UCL Neg. 4071/24, Borehole 81/43, 46.53m; XP. Fig.2b, UCL Neg. 4071/25; same specimen in Ph. Fig.3a, UCL Neg. 4071/31, Borehole 81/43, 46.53m; XP; **holotype**. Fig.3b, UCL Neg. 4071/32; same specimen in Ph.

Fig.4 (a & b): ***Calculites burnettiae* (transitional between var.A & var.B).** Fig.4a, UCL Neg. 4071/22, Borehole 81/43, 46.53m; XP. Fig.4b, UCL Neg. 4071/23; same specimen in Ph.

Fig.5 (a & b): ***Calculites burnettiae* var.B.** Fig.5a, UCL Neg. 4071/29, Borehole 81/43, 46.53m; XP. Fig.5b, UCL Neg. 4071/30; same specimen in Ph.

Fig. 6 (a & b): ***Zebrashapka vanhintei.*** Fig.6a, UCL Neg. 4021/20, Borehole 81/43, 47.54m; XP. Fig.6b, UCL Neg. 4021/19; XP, same specimen rotated 45°.

Fig. 7 (a-c): ***Clepsilithus maculosus* (sp. nov.).** Fig.7a, UCL Neg. 4071/19; Borehole 81/43, 32.80m; XP. Fig.7b, UCL Neg. 4071/20; XP, same specimen rotated 45°. Fig.7c, UCL Neg. 4071/21; same specimen in Ph.

Fig. 8 (a & b): ***Stephanolithion atmetros.*** Fig.8a, UCL Neg. 4065/27; Borehole 81/43, 90.45m; XP. Fig.8b, UCL Neg. 4065/26; same specimen in Ph.

Fig. 9 (a & b): ***Rotelapillus laffittei.*** Fig.9a, UCL Neg. 3507/3; Speeton, Bed C2B (13); XP. Fig.9b, UCL Neg. 3507/4; same specimen in Ph.

Fig. 10: ***Scapholithus fossilis.*** UCL Neg. 5313/23; Speeton, Bed C2B (16); XP.

Fig. 11 (a & b): ***Stradnerlithus silvaradius.*** Fig.11a, UCL Neg. 5012/32; Moorberg, MO5; XP. Fig.11b, UCL Neg. 5012/34; same specimen in Ph.

Fig. 12: ***Markalius* sp.** UCL Neg. 5012/9, Speeton, Bed C2C (19); XP.

Fig. 13: ***Apertasphaera jakubowskii* (sp. nov.).** UCL Neg. 3697/22, Speeton, Bed D3D; XP.

Fig. 14: ***Apertasphaera* sp..** UCL Neg. 3513/29, Speeton, Bed C2B (16); XP.

Fig. 15: ***Haqius circumradiatus.*** UCL Neg. 4094/13, Borehole 81/43, 13.70m; XP.

Fig. 16 (a & b): ***Haqius ellipticus.*** Fig.16a, UCL Neg. 4097/7, Speeton, Bed D2D; XP. Fig.16b, UCL Neg. 4097/8; same specimen in Ph.

Fig. 17: ***Discorhabdus ignotus.*** UCL Neg. 3507/19, 3507/19, Speeton, Bed C2C (19); XP.

Fig. 18: ***Crucibiscutum salebrosum.*** UCL Neg. ?; XP.

Fig. 19: ***Sollasites lowei.*** UCL Neg. 3722/2, Speeton, Bed LB3B; XP.

Fig. 20 (a & b): ***Sollasites horticus* (coccosphere).** Fig.20a, UCL Neg. 5015/17, Borehole 81/43, 7.12m; XP. Fig.20b, UCL Neg. 5015/16; same in Ph.

Fig. 21 (a & b): ***Seribiscutum primitivum.*** Fig.21a, UCL Neg. 4097/1, Heslerton Borehole, CS-5; XP. Fig.21b, UCL Neg. 4097/2; same specimen in Ph.

Plate 9

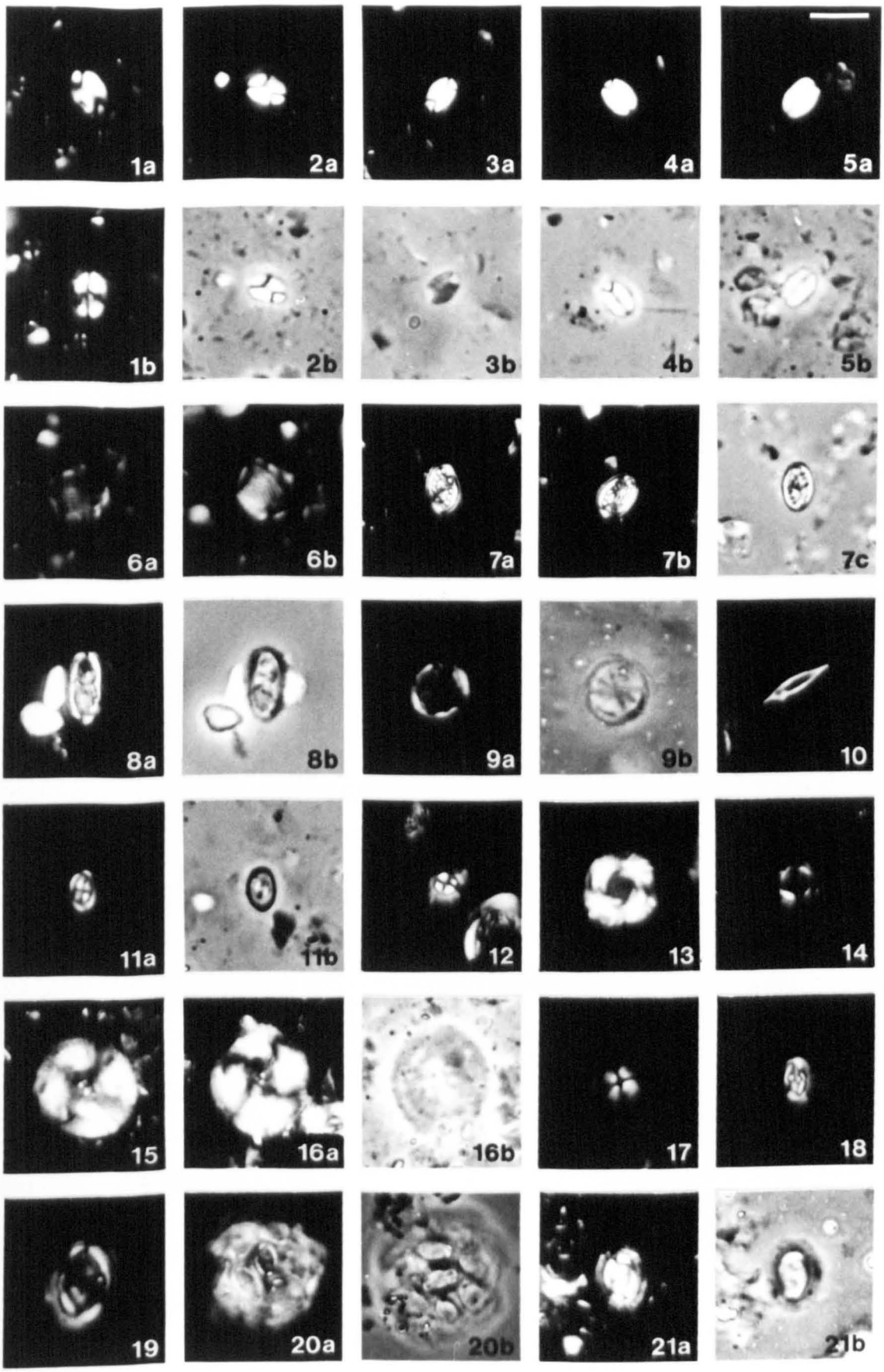

1a
2a
3a
4a
5a
1b
2b
3b
4b
5b
6a
6b
7a
7b
7c
8a
8b
9a
9b
10
11a
11b
12
13
14
15
16a
16b
17
18
19
20a
20b
21a
21b

PLATE 10

PLATE 10

Zeugrhabdotus

Scale bar at the top of each SEM = 1μm.

All LMs to same magnification (larger than in previous plates); scale bar in Fig.3b = 5μm.

P = proximal wall cycle.
D = distal wall cycle.

Figs. 1-3: ***Zeugrhabdotus noeliae.***
SEMs:
Fig.1, UCL Neg. 4062/15, Borehole 81/43, 46.53m; distal view.
Fig.2, UCL Neg. 4070/15, Borehole 81/43, 29.37m; proximal view.
LMs:
Fig.3a, UCL Neg. 4095/1, Speeton, Bed C9C (upper); XP.
Fig.3b, UCL Neg. 4095/2; XP, same specimen rotated 45°.

Figs. 4-6: ***Zeugrhabdotus erectus.***
SEMs:
Fig.4, UCL Neg. 4060/12, Borehole 81/43, 90.45m; distal view.
Fig.5, UCL Neg. 4060/16, Borehole 81/43, 90.45m; proximal view.
LMs:
Fig.6a, UCL Neg. 5005/18, Borehole 81/43, 63.60m; XP.
Fig.6b, UCL Neg. 5005/17; XP; same specimen rotated 45°.

Figs. 7-9: ***Zeugrhabdotus embergeri.***
SEMs:
Fig.7a, UCL Neg. 4076/25, Borehole 81/43, 41.16m; distal view.
Fig.7b, UCL Neg. 4076/26; same specimen (tilted).
LMs:
Fig.8, UCL Neg. 4095/15, Gault Clay (Folkestone), Bed VII; XP.
Fig.9, UCL Neg. 4095/34, Heslerton Borehole, CS-5; XP (side view).

Figs. 10-15: ***Zeugrhabdotus scutula.***
SEMs:
Fig.10a, UCL Neg. 4069/4, Borehole 81/43, 18.00m, distal view.
Fig.10b, UCL Neg. 4069/5; same specimen (tilted).
Fig.11, UCL Neg. 4062/32, Borehole 81/43, 11.92m, distal view.
Fig.12, UCL Neg. 4062/33, Borehole 81/43, 11.92m, proximal view.
LMs:
Fig.13a, UCL Neg. 4094/18, Speeton, Lower Cement Bed 49; XP.
Fig.13b, UCL Neg. 4094/17 ; XP, same specimen rotated 45°.
Fig.14, UCL Neg. 4094/23, Speeton, Lower Cement Bed 49; XP (side view).
Fig.15, UCL Neg. 4065/34, Speeton, Lower Cement Bed 49; XP.

Fig. 16: ***Loxolithus armilla.***
UCL Neg. 4076/32, Borehole 81/43, 62.38m, distal view.
(arrow indicates direction of imbrication of wall elements)

Fig. 17: ***Zeugrhabdotus* sp..**
UCL Neg. 4069/13, Borehole 81/43, 18.00m, distal view.

Fig. 18: ***Zeugrhabdotus* sp..**
UCL Neg. 4061/8, Borehole 81/43, 41.16m, distal view.

Fig. 19: ***Zeugrhabdotus diplogrammus.***
UCL Neg. 4070/16, Borehole 81/43, 29.37m, proximal view.

Plate 10

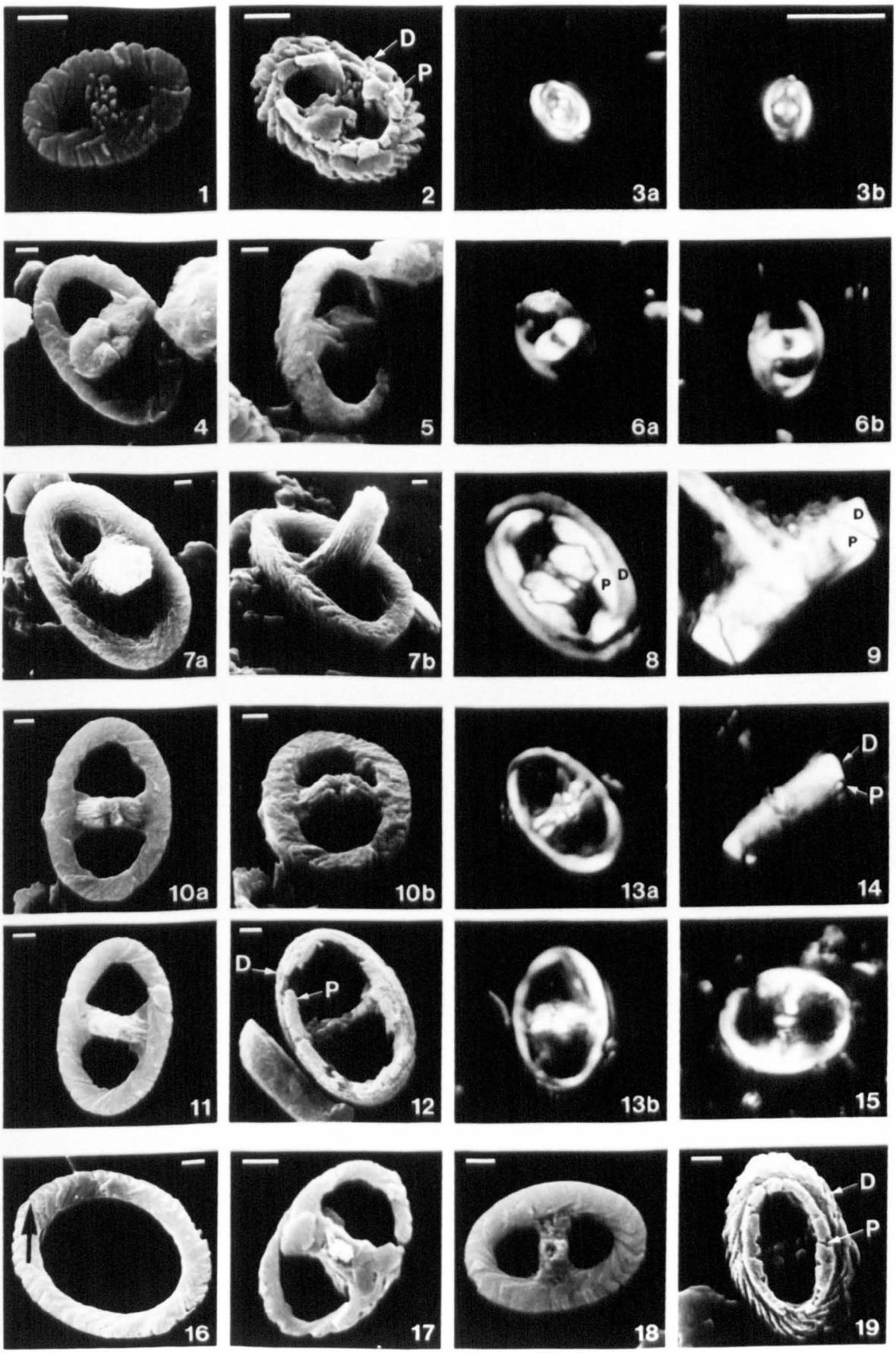

1
D
P
2
3a
3b
4
5
6a
6b
7a
7b
P
D
8
D
P
9
10a
10b
13a
D
P
14
11
D
P
12
13b
15
16
17
18
D
P
19

PLATE 11

PLATE 11

Light Micrographs; all at 2000x magnification (scale bar in Fig.2b = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Fig. 1 (a-c): ***Zeugrhabdotus noeliae.*** Fig.1a, UCL Neg. 4095/1, Speeton, Bed C9C (upper); XP. Fig.1b, UCL Neg. 4095/2; XP; same specimen rotated 45°. Fig.1c, UCL Neg. 4095/3; same specimen in Ph.

Figs. 2-3: ***Zeugrhabdotus erectus.*** Fig.2a, UCL Neg. 5005/18, Borehole 81/43, 63.60m; XP. Fig.2b, UCL Neg. 5005/19; same specimen in Ph. Fig.2c, UCL Neg. 4021/11, Borehole 81/43, 45.01m; XP.

Figs. 4-5: ***Zeugrhabdotus embergeri.*** Fig.4, UCL Neg. 4095/14, Gault Clay (Folkestone), Bed VII; XP. Fig.5, UCL Neg. 4095/34, Heslerton Borehole, CS-5; XP (side view).

Fig. 6 (a & b): ***Zeugrhabdotus diplogrammus.*** Fig.6a, UCL Neg. 3697/1, Speeton, Bed C9C; XP. Fig.6b, UCL Neg. 3697/2; XP, same specimen rotated 45°.

Fig. 7 (a & b): ***Zeugrhabdotus "elegans".*** Fig.7a, UCL Neg. 4095/20, Gault Clay (Folkestone), Bed XIII; XP. Fig.7b, UCL Neg. 4095/22; same specimen in Ph.

Fig. 8 (a-c): ***Zeugrhabdotus trivectis.*** Fig.8a, UCL Neg. 3722/31, Speeton, Bed LB4D (upper); XP. Fig.8b, UCL Neg. 3722/32; XP, same specimen rotated 45°. Fig.8c, UCL Neg. 3722/33; same specimen in Ph.

Fig. 9 (a & b): ***Tranolithus gabalus.*** Fig.9a, UCL Neg. 4094/29, Borehole 81/43, 34.11m; XP. Fig.9b, UCL Neg. 4094/30; same specimen in Ph.

Fig. 10 (a-c): ***Zeugrhabdotus xenotus.*** Fig.10a, UCL Neg. 4094/10, Heslerton Borehole, BH-2(66); XP. Fig.10b, UCL Neg. 4094/11; XP, same specimen rotated 45°. Fig.10c, UCL Neg. 4094/12; same specimen in Ph.

Figs. 11-13: ***Zeugrhabdotus scutula.*** Fig.11a, UCL Neg. 4094/17, Speeton, Lower Cement Bed 49; XP. Fig.11b, UCL Neg. 4094/18; XP, same specimen rotated 45°. Fig.11c, UCL Neg. 4094/19; same specimen in Ph. Fig.12, UCL Neg. 4065/34, Speeton, Lower Cement Bed 49; XP. Fig.13, UCL Neg. 4065/31, Speeton, Lower Cement Bed 49; XP (side view).

Fig. 14: ***Tranolithus* sp..** UCL Neg. 3515(B)/11, Speeton, Bed C7F; XP.

Fig. 15-16: ***Watznaueria ?fasciata.*** Fig.15a, UCL Neg. 5015/26, Speeton, Bed C2E (upper); XP. Fig.15b, UCL Neg. 5015/27; XP, same specimen rotated 45°. Fig.16, UCL Neg. 5015/24, Speeton, Bed C2E (upper); XP.

Fig. 17: ***Watznaueria ovata.*** UCL Neg. 5012/5, Speeton, Bed C11A; XP.

Fig. 18: ***Watznaueria barnesae.*** UCL Neg. 5012/26, Borehole 81/43, 24.90m; XP.

Fig. 19: ***Watznaueria communis.*** UCL Neg. 4097/19, Speeton, Bed LB5C.III; XP.

Fig. 20: ***Watznaueria fossacincta.*** UCL Neg. 4074/12, Heslerton Borehole, BH-2(67); XP.

Fig. 21 (a & b): ***Watznaueria britannica.*** Fig.21a, UCL Neg. 4065/24, Borehole 81/43, 90.45m; XP. Fig.21b, UCL Neg. 4065/25; XP, same specimen rotated 45°.

Plate 11

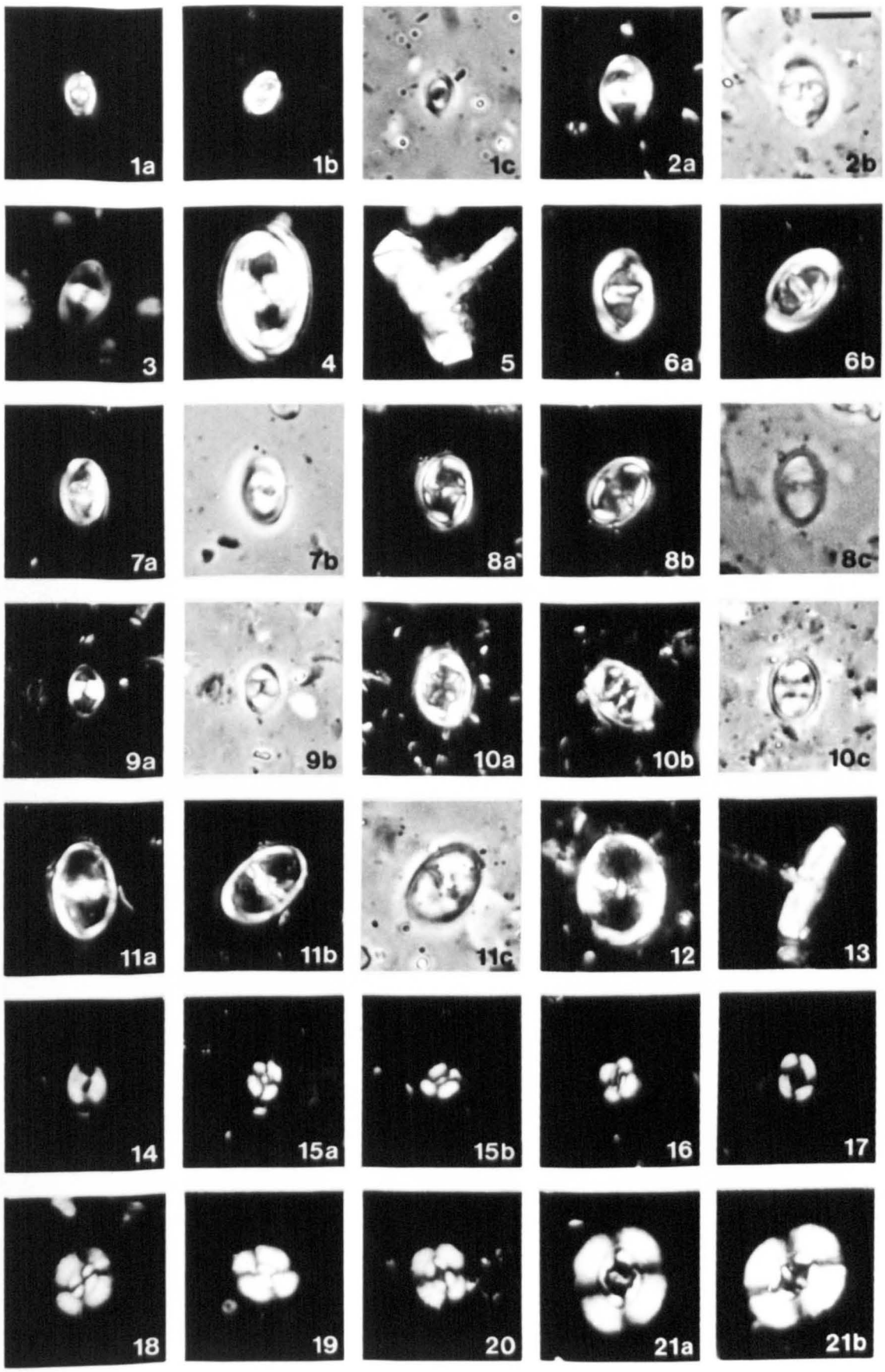

1a
1b
1c
2a
2b
3
4
5
6a
6b
7a
7b
8a
8b
8c
9a
9b
10a
10b
10c
11a
11b
11c
12
13
14
15a
15b
16
17
18
19
20
21a
21b

PLATE 12

PLATE 12

Watznaueriaceae

Scanning Electron Micrographs; scale bar at the top of each micrograph = 1μm.

Fig. 1: ***Watznaueria rawsonii.***
UCL Neg. 4073/1, Borehole 81/43, 64.79m, distal view.

Fig. 2: ***Watznaueria britannica.***
UCL Neg. 4060/17, Borehole 81/43, 90.45m, distal view.

Figs. 3-5: ***Watznaueria fossacincta.***
Fig.3, UCL Neg. 4076/2, Borehole 81/43, 41.16m, proximal view (partial coccosphere).
Fig.4, UCL Neg. 4060/21, Borehole 81/43, 41.16m, coccosphere.
Fig.5, UCL Neg. 4067/10, Speeton, Bed D1, coccosphere.

Fig. 6: ***Watznaueria barnesae.***
UCL Neg. 4069/2, Borehole 81/43, 18.00m, coccosphere.

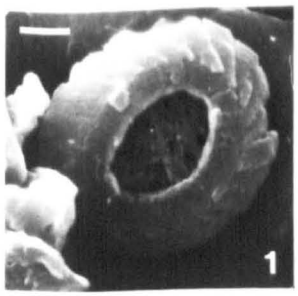
Fig. 7: ***Haqius circumradiatus.***
UCL Neg. 4062/16, Borehole 81/43, 46.53m, distal view.

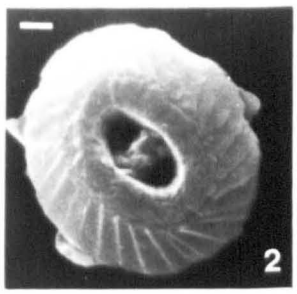
Figs. 8-9: ***Haqius ellipticus.***
Fig.8, UCL Neg. 4063/27, Borehole 81/43, 41.16m, proximal view.
Fig.9, UCL Neg. 4081/22, Borehole 81/43, 29.37m, distal view.

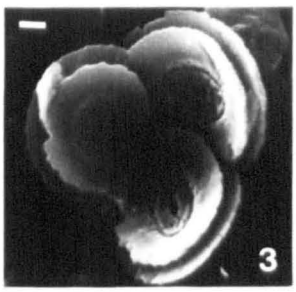
Figs. 10-14: ***Apertasphaera jakubowskii* (sp. nov.).**
Fig.10, UCL Neg. 4073/24, Borehole 81/43, 64.79m, distal view (broken specimen), **isotype.**
Fig.11, UCL Neg. 4068/26, Borehole 81/43, 18.00m, side view, **holotype.**
Fig.12, UCL Neg. 4073/5, Borehole 81/43, 64.79m, side view.
Fig.13, UCL Neg. 4068/22, Borehole 81/43, 18.00m, proximal view (etched specimen).
Fig.14a, UCL Neg. 4073/9, Borehole 81/43, 64.79m, proximal view, **isotype.**
Fig.14b, UCL Neg. 4073/10, same specimen (tilted).

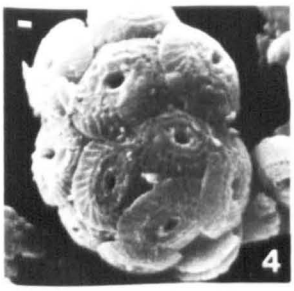
Figs. 15-16: ***Apertasphaera* sp..**
Fig. 15, UCL Neg. 4073/21, Borehole 81/43, 64.79m, proximal view.
Fig.16a, UCL Neg. 4073/16, Borehole 81/43, 64.79m, distal view.
Fig.16b, UCL Neg. 4073/17, same specimen (tilted).

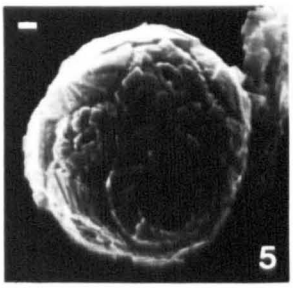
Plate 12

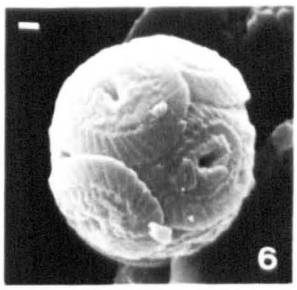

1

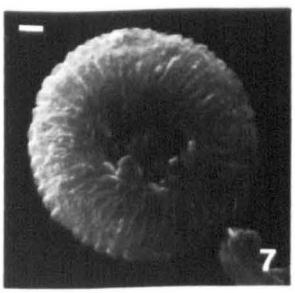

2

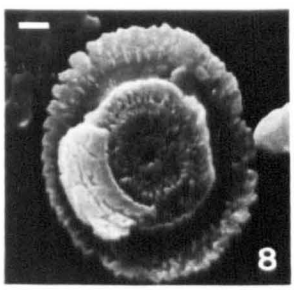

3

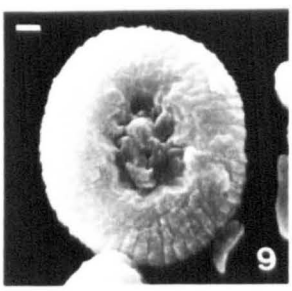

4

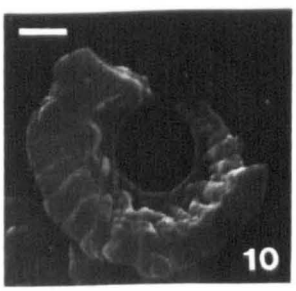

5

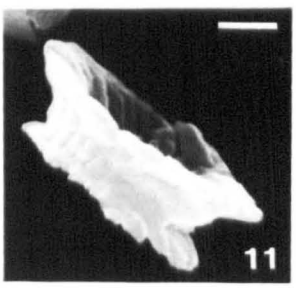

6

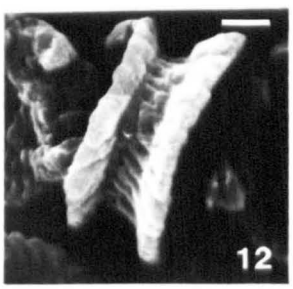

7

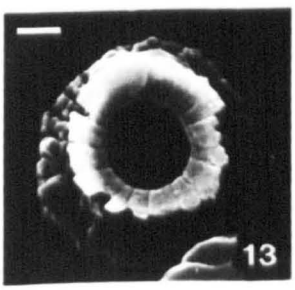

8

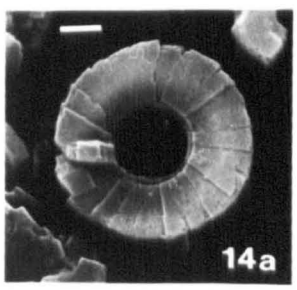

9

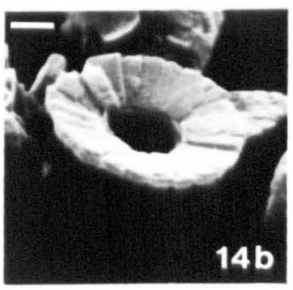

10

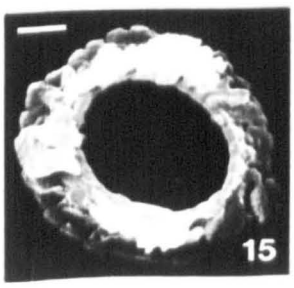

11

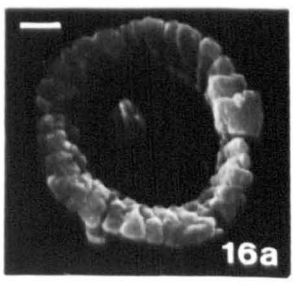

12


13


14a


14b


15


16a

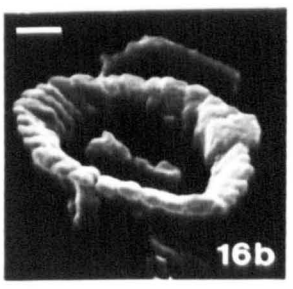

16b

PLATE 13

PLATE 13

Cyclagelosphaera

Scale bars in Figs.1 & 6 = 5μm; those in the other SEMs = 1μm.

All light micrographs (LMs) are at 2000x magnification (scale bar in Fig.4 = 5μm).
XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Figs. 1-5: ***Cyclagelosphaera margerelii.***

SEMs:
Fig.1, UCL Neg. 4073/20, Borehole 81/43, 64.79m; coccosphere.
Fig.2, UCL Neg. 4070/8, Borehole 81/43, 64.79m; distal view.
Fig.3, UCL Neg. 4073/8, Borehole 81/43, 64.79m; distal view (tilted).

LMs:
Fig.4, UCL Neg. 5012/4, Speeton, Bed C11A; XP.
Fig.5, UCL Neg. 5012/2, Speeton, Bed C11A; XP.

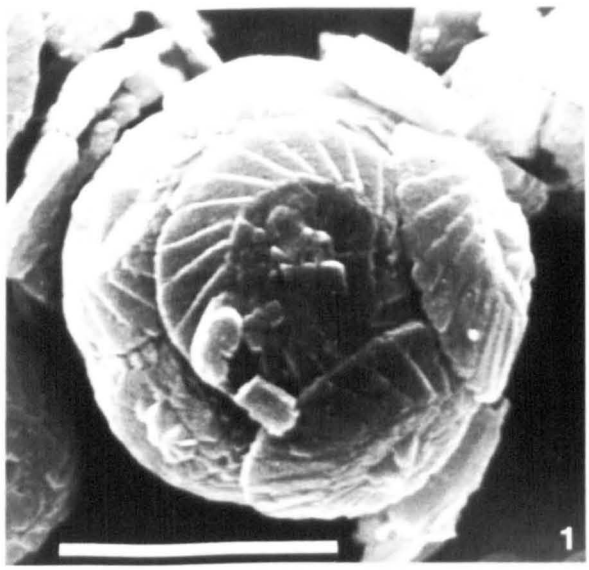
Figs. 6-9: ***Cyclagelosphaera papilla* (sp. nov.).**

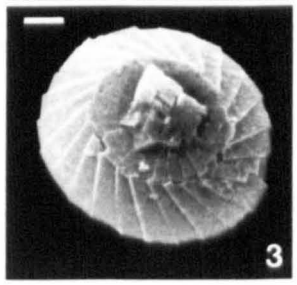
SEMs:
Fig.6, UCL Neg. 4074/17, Borehole 81/43, 17.00m; coccosphere, **holotype**.
Fig.7a, UCL Neg. 4060/10, Borehole 81/43, 17.00m; distal view; **isotype**.
Fig.7b, UCL Neg. 4060/11; same specimen (tilted).
Fig.8, UCL Neg. 4060/34, Borehole 81/43, 41.16m; distal view; **isotype**.

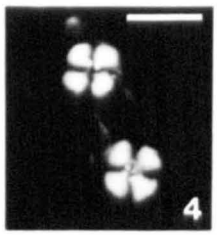
LMs:
Fig.9a, UCL Neg. 4097/22, Borehole 81/43, 12.79m; XP.
Fig.9b, UCL Neg. 4097/23; XP; same specimen at a different level of focus.
Fig.9c, UCL Neg. 4097/24; same specimen in Ph.

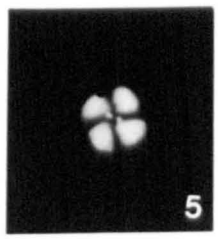
Fig.10a, UCL Neg. 4094/15, Borehole 81/43, 13.70m; XP.
Fig.10b, UCL Neg. 4094/16; same specimen in Ph.

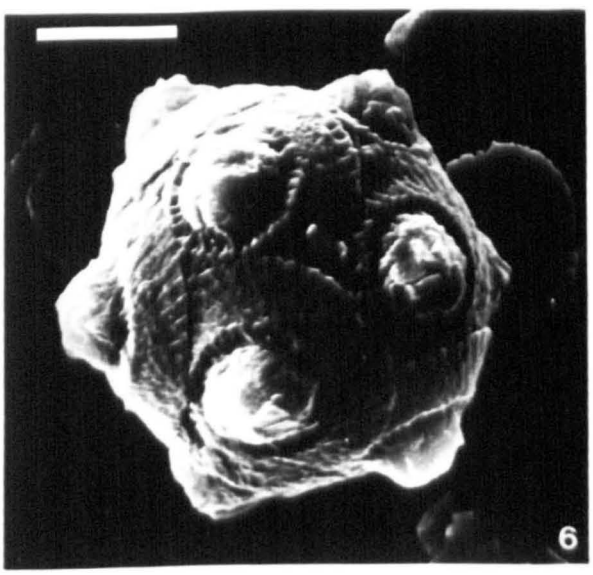
Plate 13

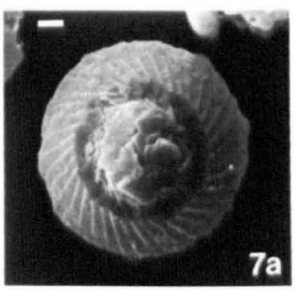


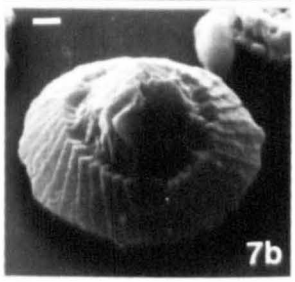


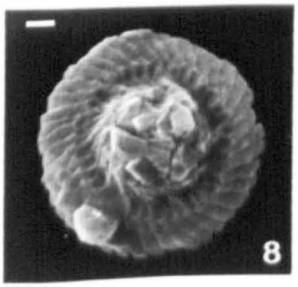


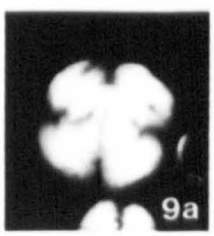


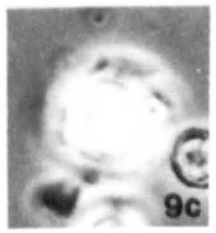












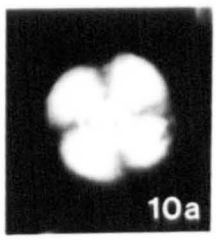


PLATE 14

PLATE 14

Scale bar at the top of each SEM = 1μm.

All light micrographs (LMs) are at 2000x magnification (scale bar in Fig.5c = 5μm).
XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Figs. 1-6: ***Tubodiscus parvus*** **(sp. nov.).**

SEMs:
Fig.1a, UCL Neg. 4081/2, Borehole 81/43, 7.12m; distal view (length=6μ).
Fig.1b, UCL Neg. 4081/3; same specimen tilted.
Fig.2, UCL Neg. 4073/28, Borehole 81/43, 29.37m; proximal view.
Fig.3, UCL Neg. 4081/6, Borehole 81/43, 7.12m; oblique proximal view (length=6.5μ).
Fig.4, UCL Neg. 4076/5, Borehole 81/43, 41.16m; proximal views.

LMs:
Fig.5a, UCL Neg. 5015/18, Borehole 81/43, 7.12m; XP; **holotype**.
Fig.5b, UCL Neg. 5015/19; XP, same specimen rotated 45°.
Fig.5c, UCL Neg. 5015/20; same specimen in Ph.
Fig.6a, UCL Neg. 5015/21, Borehole 81/43, 7.12m; XP; **isotype**.
Fig.6b, UCL Neg. 5015/22; XP, same specimen rotated 45°.
Fig.6c, UCL Neg. 5015/23; same specimen in Ph.

Figs. 7 & 10: ***Tubodiscus jurapelagicus.***

LMs:
Fig.7a, UCL Neg. 5015/12, Speeton, Bed C2C (17); XP.
Fig.7b, UCL Neg. 5015/13; XP, same specimen at a different level of focus - note tube cycle.
Fig.7c, UCL Neg. 5015/14; XP, same specimen rotated 45°.
Fig.7d, UCL Neg. 5015/15; same specimen in Ph.

SEM:
Fig.10, UCL Neg. 4081/29, Borehole 81/43, 29.37m; proximal view.

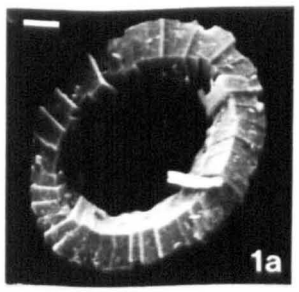
Fig. 8 (a & b): ***Tubodiscus verenae.***
Fig.8a, UCL Neg. 4021/32, Borehole 81/43, 38.66m; XP.
Fig.8b, UCL Neg. 4021/31; XP, same specimen rotated 45°.

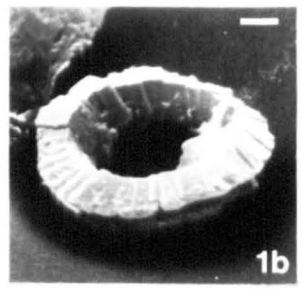
Figs. 9, 11 & 12: ***Manivitella pemmatoidea.***

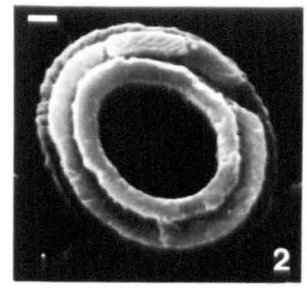
LMs:
Fig.9a, UCL Neg. 4089/25, Gault Clay (Folkestone), Bed VII (upper); XP.
Fig.9b, UCL Neg. 4089/26; same specimen in Ph.

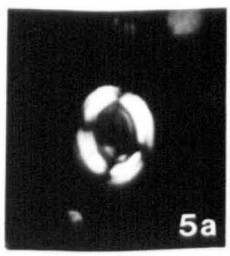
SEMs:
Fig.11, UCL Neg. 4081/23, Borehole 81/43, 29.37m; proximal view.
Fig.12, UCL Neg. 4060/32, Borehole 81/43, 41.16m; distal view.

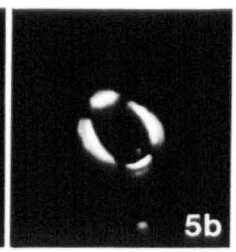
Plate 14

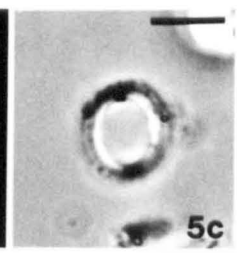

1a

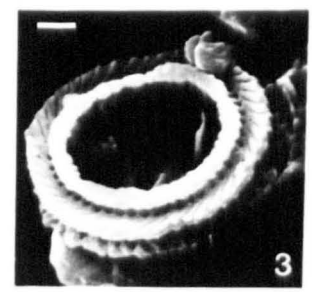

1b

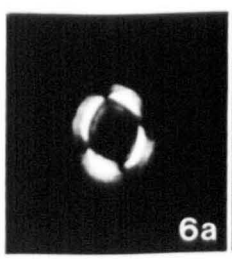

2

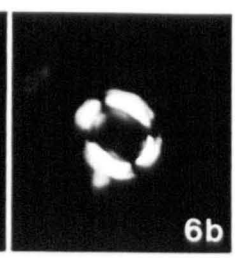

5a

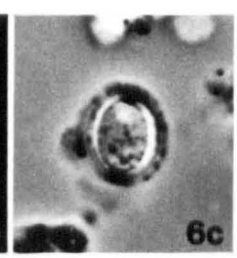

5b

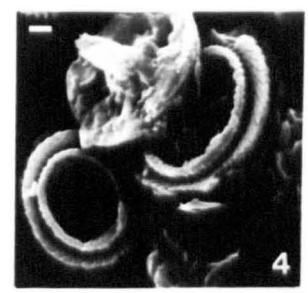

5c

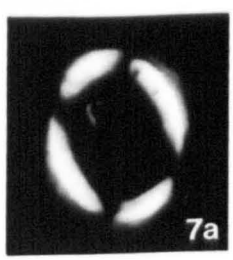

3

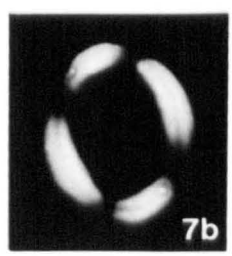

6a

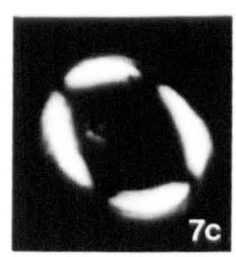

6b

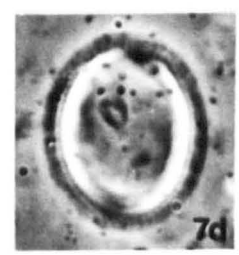

6c

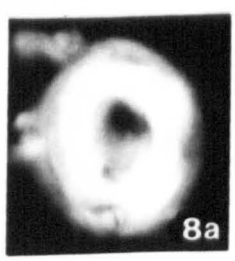

4

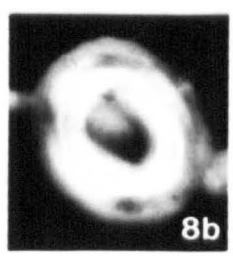

7a

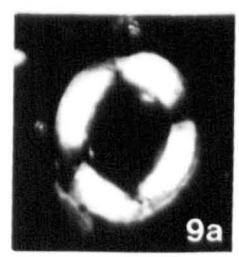

7b

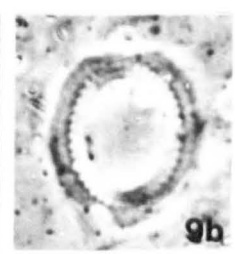

7c

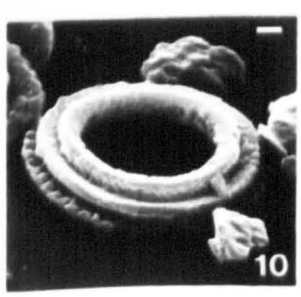

7d

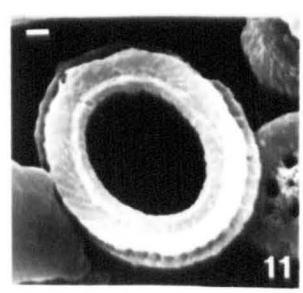

8a


8b


9a


9b


10


11

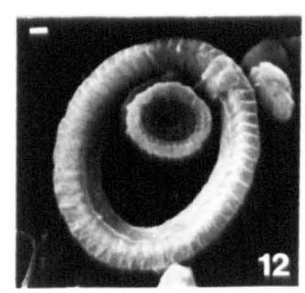

12

PLATE 15

PLATE 15

Cretarhabdaceae

Scanning Electron Micrographs; scale bar at the top of each micrograph = 1μm.

Fig. 1: ***Cretarhabdus octofenestratus.***
UCL Neg. 4062/3, Borehole 81/43, 46.53m, distal view.

Fig. 2: ***Cretarhabdus angustiforatus.***
UCL Neg. 4060/8, Borehole 81/43, 17.00m, distal view.

Fig. 3: ***Cretarhabdus crenulatus.***
UCL Neg. 4061/18, Borehole 81/43, 32.80m, distal view.

Fig. 4: ***Cretarhabdus surirellus.***
UCL Neg. 4070/13, Borehole 81/43, 29.37m, distal view.

Figs. 5 & 6: ***Cretarhabdus madingleyensis.***
Fig.5, UCL Neg. 4068/18, Borehole 81/43, 18.00m, distal view.
Fig.6, UCL Neg. 4076/29, Borehole 81/43, 41.16m, distal view.

Figs. 7-9: ***Cretarhabdus conicus.***
Fig.7, UCL Neg. 4069/15, Borehole 81/43, 18.00m, distal view.
Fig.8, UCL Neg. 4061/17, Borehole 81/43, 32.80m, distal view.
Fig.9, UCL Neg. 4069/16, Borehole 81/43, 18.00m, distal view (tilted).

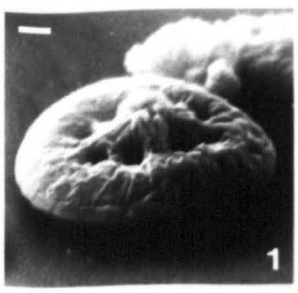
Figs. 10 & 12: ***Cretarhabdus radiatus.***
Fig.10a, UCL Neg. 4069/11, Borehole 81/43, 18.00m, terminal calyx only (in proximal view).
Fig.10b, UCL Neg. 4069/12, same specimen (tilted).
Fig.12a, UCL Neg. 4069/17, Borehole 81/43, 18.00m, side view of complete coccolith.
Fig.12b, UCL Neg. 4069/17, proximal view of same specimen.

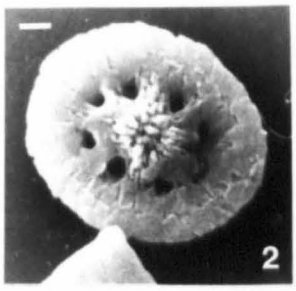
Fig. 11: ***Cretarhabdus inequalis.***
UCL Neg. 4068/30, Borehole 81/43, 18.00m, distal view.

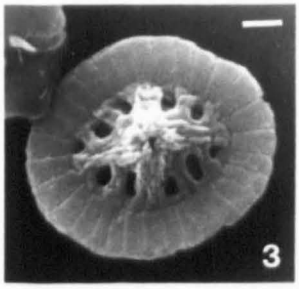
Fig. 13: ***Cruciellipsis cuvillieri.***
UCL Neg. 4067/8, Speeton, Bed D1, distal view.

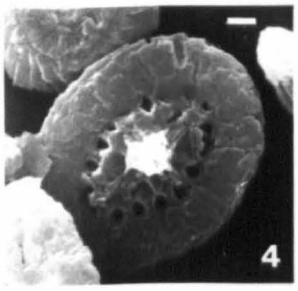
Figs. 14 & 15: ***Speetonia colligata.***
Fig.14a, UCL Neg. 4074/5, Borehole 81/43, 32.80m, distal view.
Fig.14b, UCL Neg. 4074/6, same specimen (tilted).
Fig.15, UCL Neg. 4060/25, Borehole 81/43, 41.16m, proximal view.

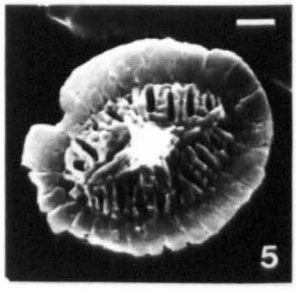
Plate 15

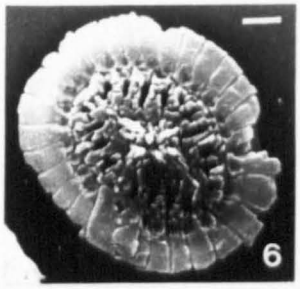

1

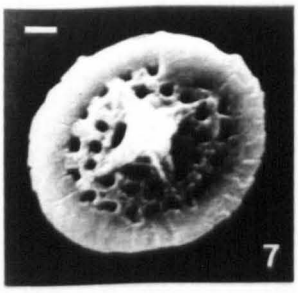

2

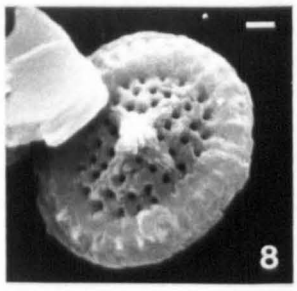

3

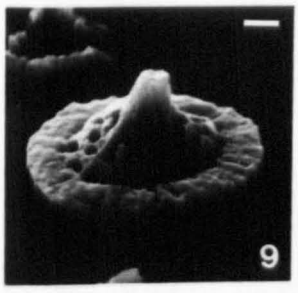

4

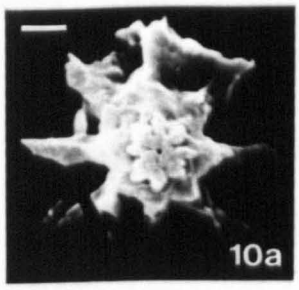

5

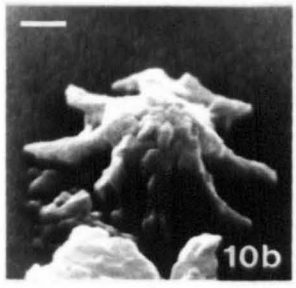

6

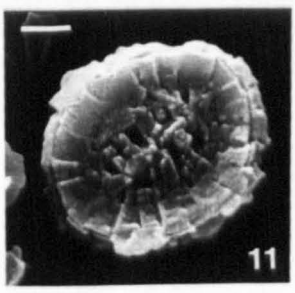

7

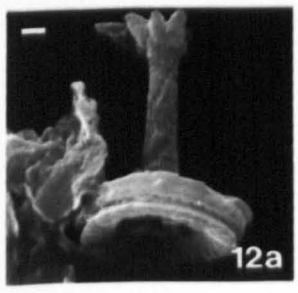

8

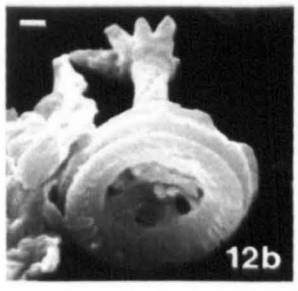

9


10a

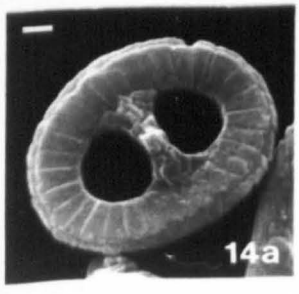

10b

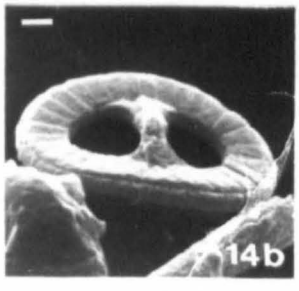

11


12a


12b


13


14a


14b

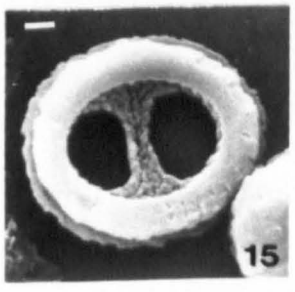

15

PLATE 16

PLATE 16

Light Micrographs; all at 2000x magnification (scale bar in Fig.4 = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Fig. 1: ***Helenea chiastia.*** UCL Neg. 3722/28, Speeton, Bed LB4D (upper); XP, distal focus (note four-part distal process).

Fig. 2: ***Helenea staurolithina.*** UCL Neg. 5012/17, Borehole 81/43, 13.70m; XP, note absence of prominent distal process, and small "feet" supporting the long-axial cross-bars.

Fig. 3 (a & b): ***Cretarhabdus octofenestratus.*** Fig.3a, UCL Neg.5005/23, Borehole 81/43, 44.46m; XP. Fig.3b, UCL Neg. 5005/24; XP, same specimen rotated 45°.

Fig. 4: ***Cretarhabdus angustiforatus.*** UCL Neg. 3722/23, Speeton, Bed LB4D (upper); XP.

Fig. 5 (a & b): ***Cretarhabdus radiatus*** (partial; radiating calyx of distal process). Fig.5a, UCL Neg. 5005/27, Speeton, Bed LB1F (12); XP. Fig.5b, UCL Neg. 5005/28; same specimen in Ph.

Fig. 6 (a-c): ***Cretarhabdus inequalis.*** Fig.6a, UCL Neg. 4065/10, Borehole 81/43, 18.00m; XP. Fig.6b, UCL Neg. 4065/14; XP, same specimen rotated. Fig.6c, UCL Neg. 4065/13; same specimen in Ph.

Fig. 7: ***Cretarhabdus conicus.*** UCL Neg. 3513/7, Speeton, Bed C2B (16); XP.

Fig. 8 (a & b): ***Cretarhabdus madingleyensis.*** Fig.8a, UCL Neg. 4071/13, Borehole 81/43, 11.92m; XP. Fig.8b, UCL Neg. 4071/14; same specimen in Ph.

Fig. 9 (a & b): ***Cruciellipsis cuvillieri.*** Fig.9a, UCL Neg. 5005/3, Speeton, Bed D1; XP. Fig.9b, UCL Neg. 5005/5; same specimen in Ph.

Fig. 10 (a & b): ***Grantarhabdus meddii.*** Fig.10a, UCL Neg. 4097/31, Borehole 81/43, 12.79m; XP. Fig.10b, UCL Neg. 4097/32; same specimen in Ph.

Fig. 11 (a & b): ***Grantarhabdus coronadventis.*** Fig.11a, UCL Neg. 3315/17, Gault Clay (Folkestone), Bed X; XP. Fig.11b, UCL Neg. 3315/18; same specimen in Ph.

Fig. 12: ***Flabellites oblongus.*** UCL Neg. 5012/11, Heslerton Borehole, BH-2(55); XP.

Fig. 13 (a & b): ***Speetonia colligata.*** Fig.13a, UCL Neg. 4023/16, Borehole 81/43, 41.16m; XP. Fig.13b, UCL Neg. 4023/17; XP, same specimen rotated 45° (note the flared ends of the bridge-forming bars).

Fig. 14: ***Pickelhaube furtiva.*** UCL Neg. 4024/7, Speeton, Bed C8B (1); XP.

Fig. 15 (a & b): ***Hemipodorhabdus gorkae.*** Fig.15a, UCL Neg. 4094/26, Borehole 81/43, 34.11m; XP. Fig.15b, UCL Neg. 4094/28; same specimen in Ph.

Fig. 16 (a & b): ***Axopodorhabdus dietzmannii.*** Fig.16a, UCL Neg. 3722/4, Speeton, Bed LB3B; XP. Fig.16b, UCL Neg. 3722/5; same specimen in Ph.

Fig. 17 (a & b): ***Axopodorhabdus albianus.*** Fig.17a, UCL Neg. 3315/19, Gault Clay (Folkestone), Bed X; XP. Fig.17b, UCL Neg. 3315/20; same specimen in Ph.

Figs. 18 & 19: ***Ethmorhabdus hauterivianus.*** Fig.18, UCL Neg. 3723/26, Speeton, Bed C9C; Ph, note hollow central process and perforate membrane. Fig.19a, UCL Neg. 3515(A)/16, Speeton, Bed C8B (5); XP. Fig.19b, UCL Neg. 3515(A)/17; same specimen in Ph (typical preservation - central membrane missing/obscured).

Fig. 20 (a-c): ***Percivalia fenestrata.*** Fig.20a, UCL Neg. 4097/25, Borehole 81/43, 12.79m; XP. Fig.20b, UCL Neg. 4097/26; XP, same specimen rotated 45°. Fig.20c, UCL Neg. 4097/27; same specimen in Ph.

Plate 16

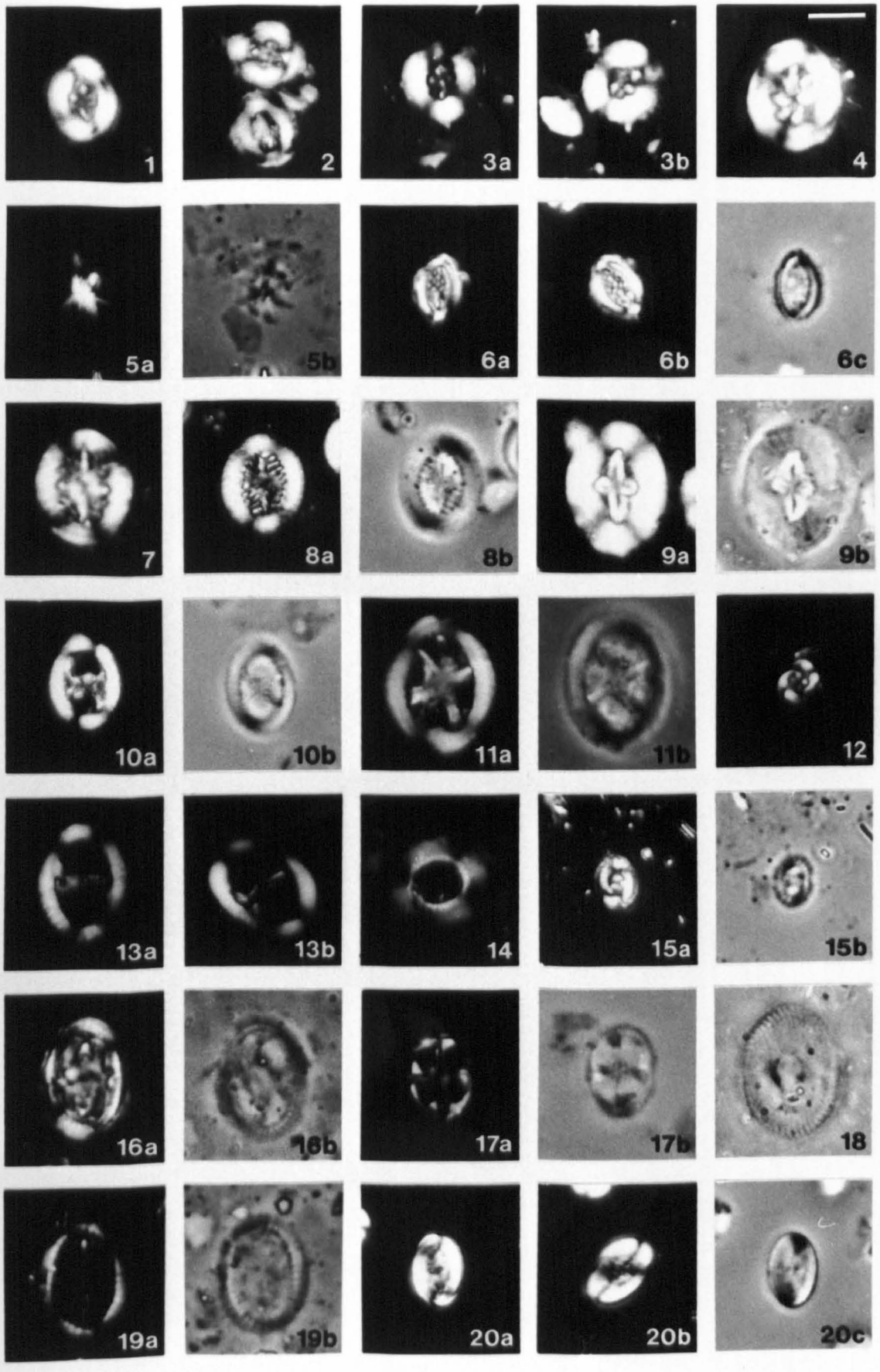

1
2
3a
3b
4
5a
5b
6a
6b
6c
7
8a
8b
9a
9b
10a
10b
11a
11b
12
13a
13b
14
15a
15b
16a
16b
17a
17b
18
19a
19b
20a
20b
20c

PLATE 17

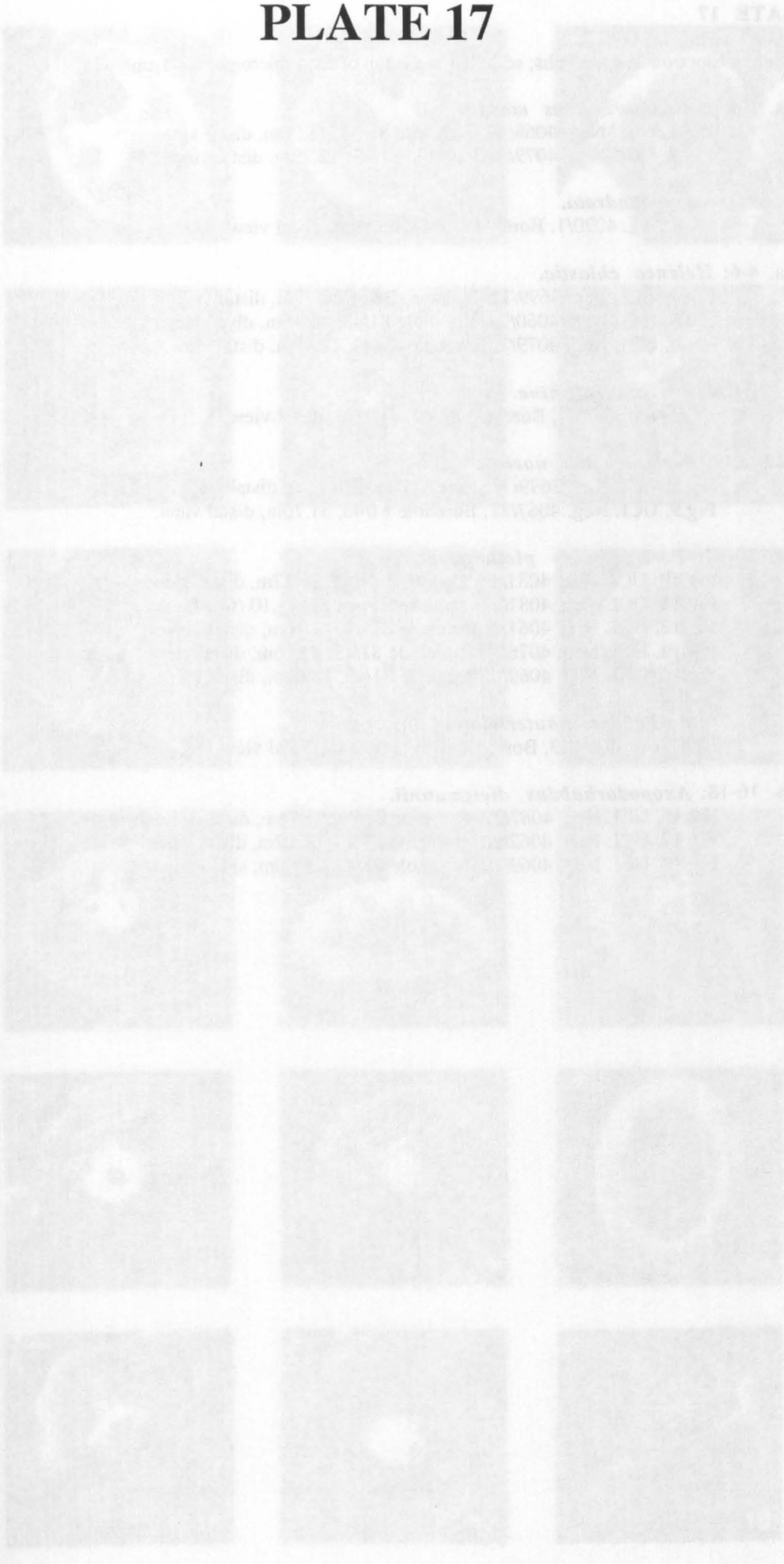


PLATE 17

Scanning Electron Micrographs; scale bar at the top of each micrograph = 1μm.

Figs. 1 & 2: ***Grantarhabdus meddii.***
Fig.1, UCL Neg. 4068/19, Borehole 81/43, 18.00m, distal view.
Fig.2, UCL Neg. 4079/5, Borehole 81/43, 12.79m, distal view.

Fig. 3: ***Helenea quadrata.***
UCL Neg. 4070/1, Borehole 81/43, 63.99m, distal view.

Figs. 4-6: ***Helenea chiastia.***
Fig.4, UCL Neg. 3699/11, Speeton, Bed C2B (14), distal view.
Fig.5, UCL Neg. 4060/24, Borehole 81/43, 41.16m, distal view.
Fig.6, UCL Neg. 4079/7, Borehole 81/43, 12.79m, distal view.

Fig. 7: ***Helenea staurolithina.***
UCL Neg. 4076/1, Borehole 81/43, 41.16m, distal view.

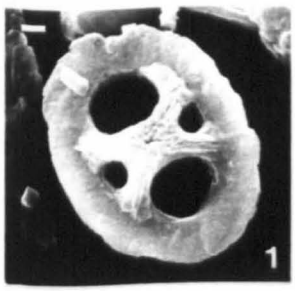
Fig. 8 & 9: ***Perissocyclus noelae.***
Fig.8, UCL Neg. 3699/7, Speeton, Bed C2B (14), distal view.
Fig.9, UCL Neg. 4067/21, Borehole 81/43, 31.76m, distal view.

Figs. 10-14: ***Perissocyclus plethotretus.***
Fig.10, UCL Neg. 4081/13, Borehole 81/43, 29.37m, distal view.
Fig.11, UCL Neg. 4081/14, same specimen as Fig.10 (tilted).
Fig.12, UCL Neg. 4061/3, Borehole 81/43, 41.16m, distal view.
Fig.13, UCL Neg. 4076/16, Borehole 81/43, 41.16m, distal view.
Fig.14, UCL Neg. 4069/3, Borehole 81/43, 18.00m, distal view.

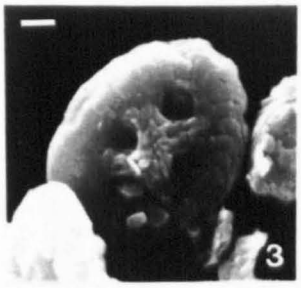
Fig. 15: ***Ethmorhabdus hauterivianus.***
UCL Neg. 4069/13, Borehole 81/43, 18.00m, distal view.

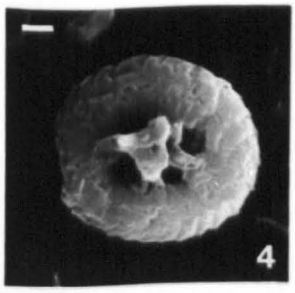
Figs. 16-18: ***Axopodorhabdus dietzmannii.***
Fig.16, UCL Neg. 4067/22, Borehole 81/43, 31.76m, distal view (broken specimen).
Fig.17, UCL Neg. 4062/26, Borehole 81/43, 63.02m, distal view.
Fig.18, UCL Neg. 4069/19, Borehole 81/43, 18.00m, side view.

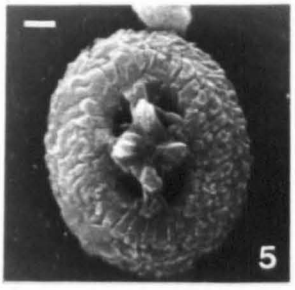
Plate 17

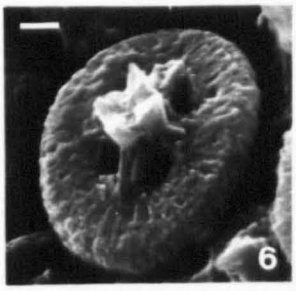

1


2

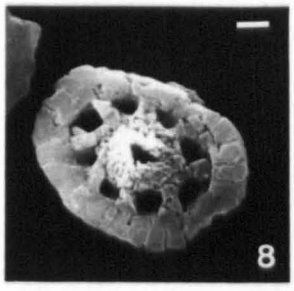

3

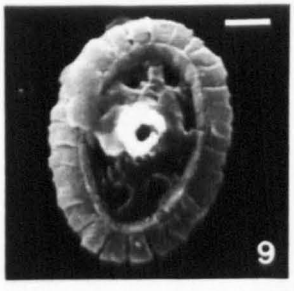

4

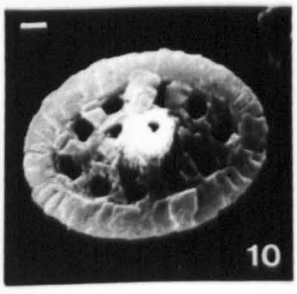

5

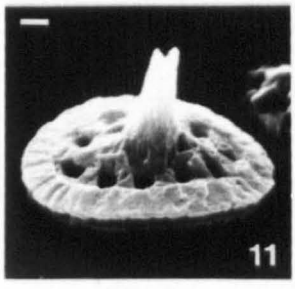

6

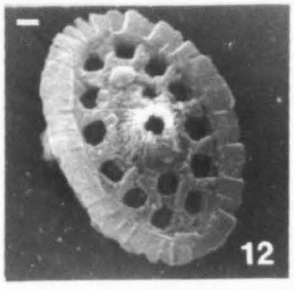

7

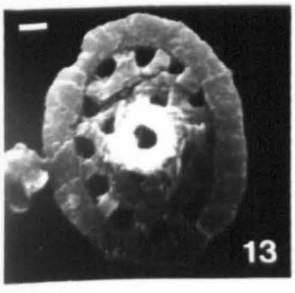

8

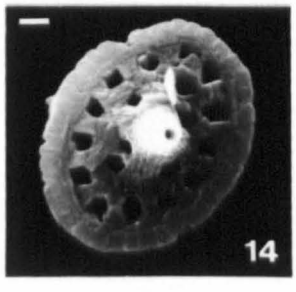

9

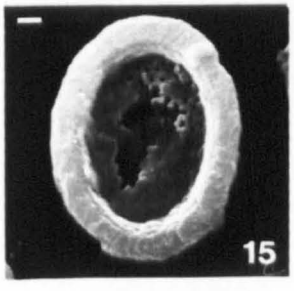

10

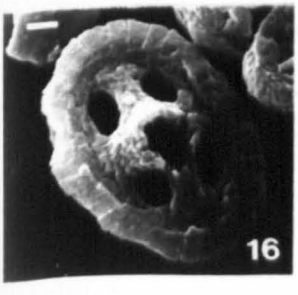

11

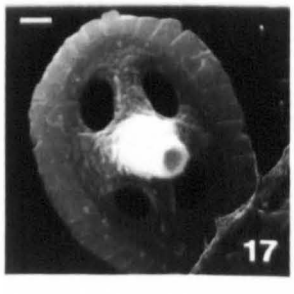

12


13


14


15


16


17

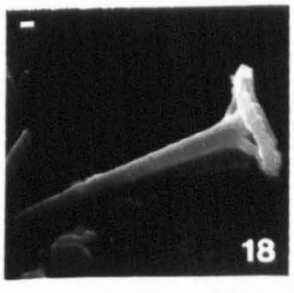

18

PLATE 18

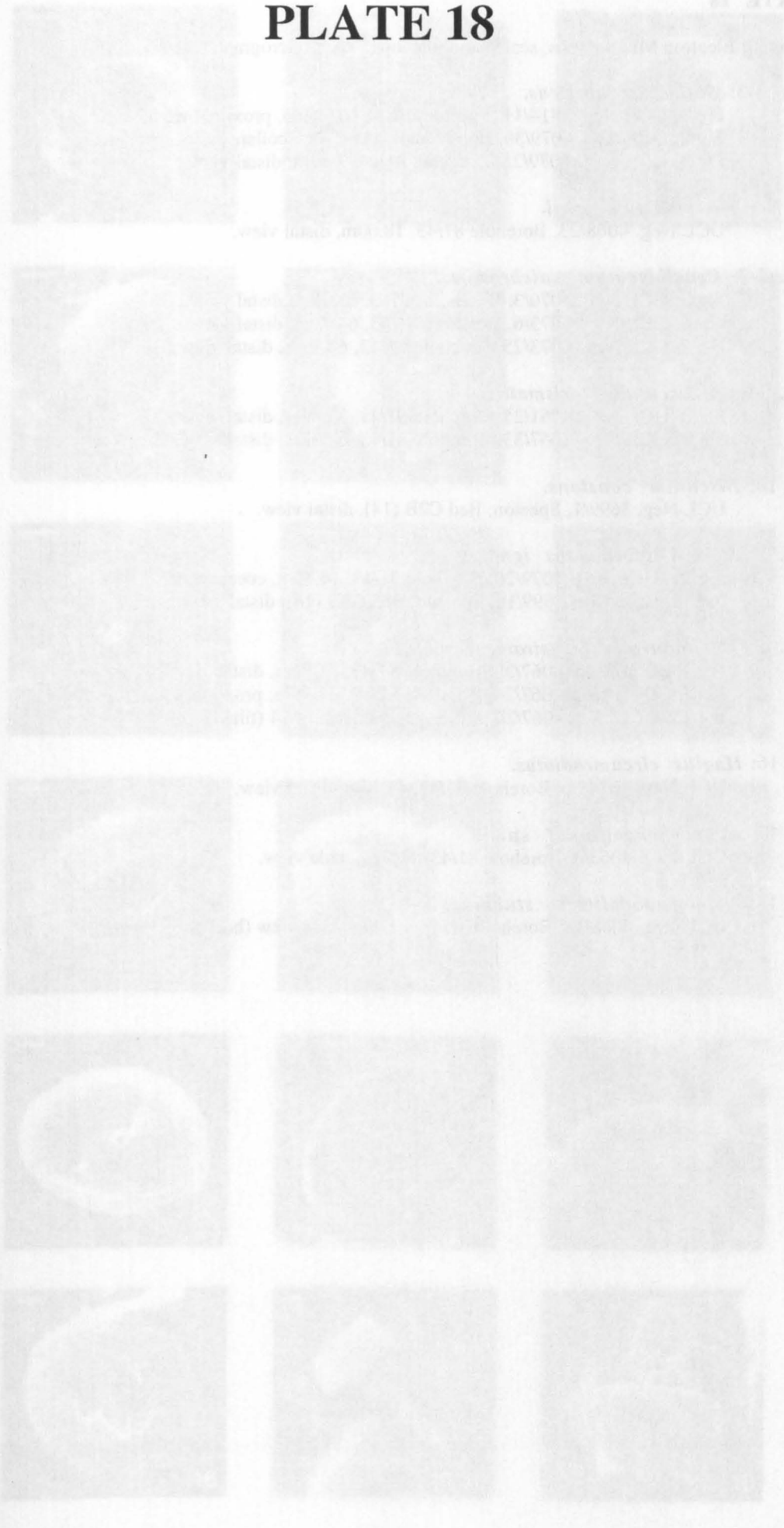


PLATE 18

Scanning Electron Micrographs; scale bar at the top of each micrograph = 1μm.

Figs. 1-3: ***Sollasites horticus.***
Fig.1, UCL Neg. 3814/11, Speeton, Bed LB1F (13), proximal view.
Fig.2, UCL Neg. 4079/30, Borehole 81/43, 7.12m, collapsed coccosphere.
Fig.3, UCL Neg. 4079/28, Borehole 81/43, 7.12m, distal view.

Fig. 4: ***Crucibiscutum hayi.***
UCL Neg. 4068/23, Borehole 81/43, 18.00m, distal view.

Figs. 5-7: ***Crucibiscutum salebrosum.***
Fig.5, UCL Neg. 4070/3, Borehole 81/43, 63.99m, distal view.
Fig.6, UCL Neg. 4073/6, Borehole 81/43, 64.79m, distal view.
Fig.7, UCL Neg. 4073/25, Borehole 81/43, 64.79m, distal view.

Figs. 8 & 9: ***Biscutum ?erismatum.***
Fig.8, UCL Neg. 4061/25, Borehole 81/43, 32.80m, distal view.
Fig.9, UCL Neg. 4067/33, Borehole 81/43, 62.38m, distal view.

Fig. 10: ***Biscutum constans.***
UCL Neg. 3699/1, Speeton, Bed C2B (14), distal view.

Figs. 11 & 12: ***Discorhabdus ignotus.***
Fig.11, UCL Neg. 4079/20, Borehole 81/43, 14.70m, coccosphere.
Fig.12, UCL Neg. 3699/16, Speeton, Bed C2B (14), distal view.

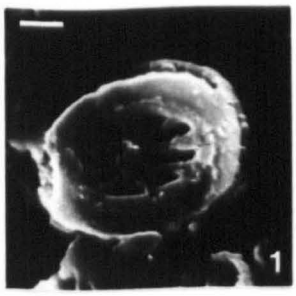
Figs. 13-15: ***Percivalia fenestrata.***
Fig.13, UCL Neg. 4067/30, Borehole 81/43, 31.76m, distal view.
Fig.14, UCL Neg. 4067/24, Borehole 81/43, 31.76m, proximal view.
Fig.15, UCL Neg. 4067/26, same specimen as Fig.14 (tilted).

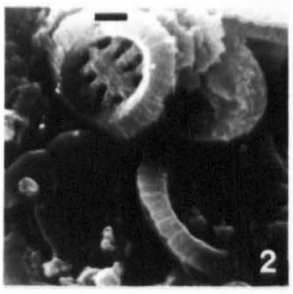
Fig. 16: ***Haqius circumradiatus.***
UCL Neg. 4074/36, Borehole 81/43, 41.16m, distal view.

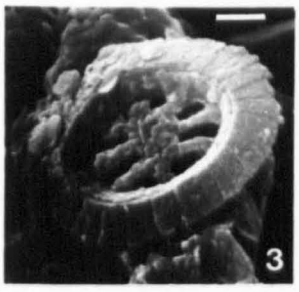
Fig. 17: ***Neoparhabdolithus?* sp..**
UCL Neg. 4063/6, Borehole 81/43, 11.92m, side view.

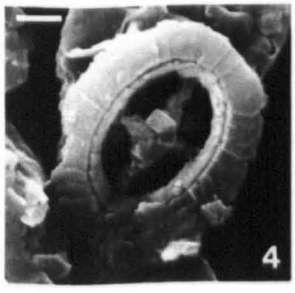
Fig. 18: ***Neoparhabdolithus stubbingsii.***
UCL Neg. 4068/11, Borehole 81/43, 18.00m, side view (broken specimen).

Plate 18

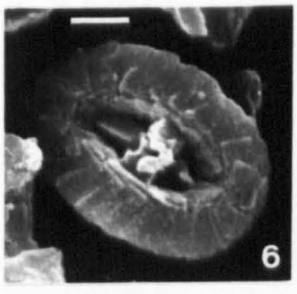

1

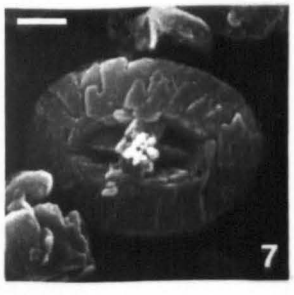

2

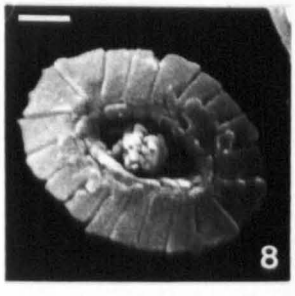

3

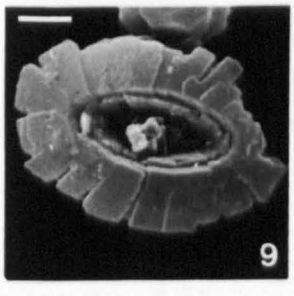

4

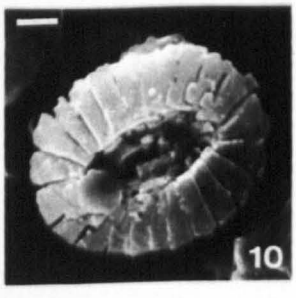

5

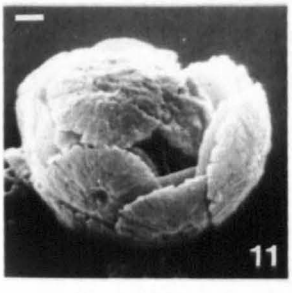

6

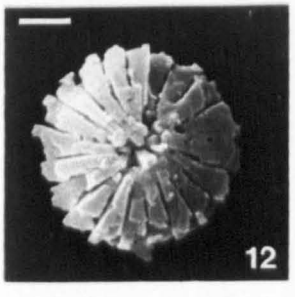

7

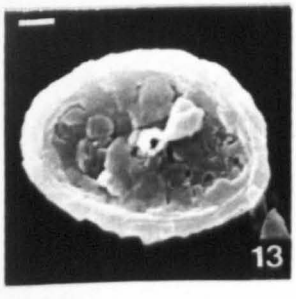

8

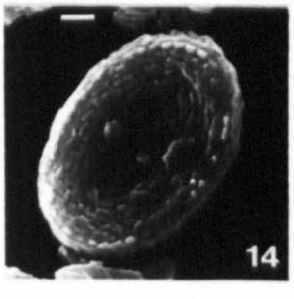

9

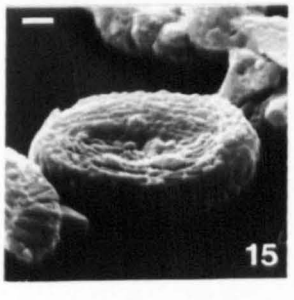

10

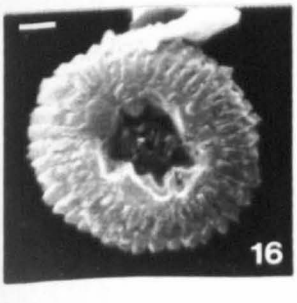

11

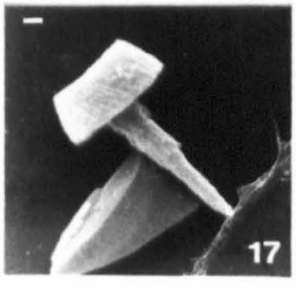

12


13


14


15


16


17

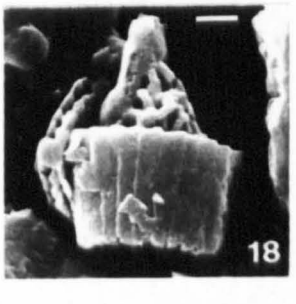

18

PLATE 19

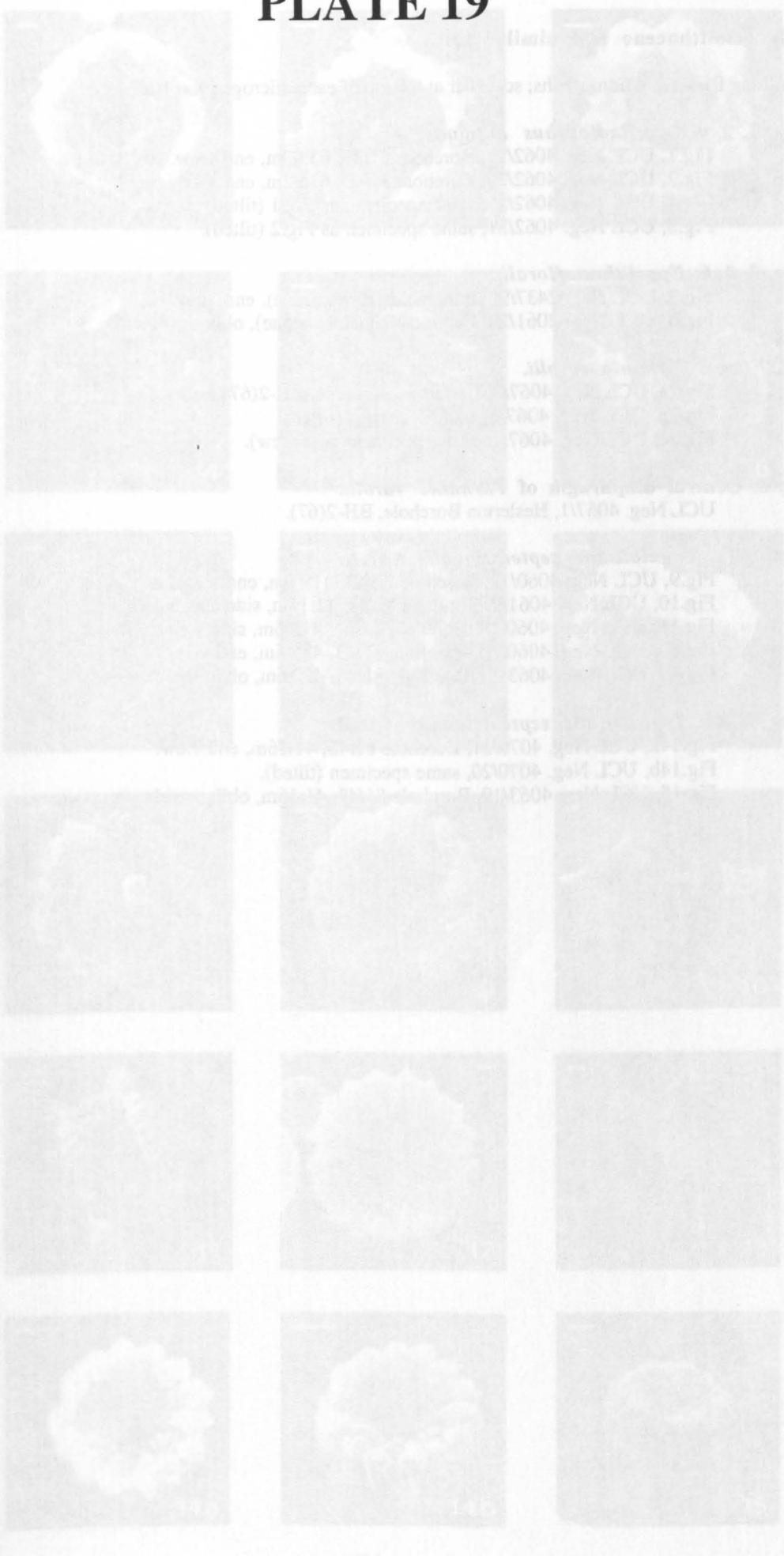


PLATE 19

Polycyclolithaceae and similar forms

Scanning Electron Micrographs; scale bar at the top of each micrograph = 1μm.

Figs. 1, 2, 4 & 5: ***Radiolithus antiquus.***
Fig.1, UCL Neg. 4062/27, Borehole 81/43, 63.02m, end view.
Fig.2, UCL Neg. 4062/30, Borehole 81/43, 63.02m, end view.
Fig.4, UCL Neg. 4062/29, same specimen as Fig.1 (tilted).
Fig.5, UCL Neg. 4062/31, same specimen as Fig.2 (tilted).

Figs. 3 & 6: ***Eprolithus floralis.***
Fig.3, UCL Neg. 2437/9, Cenomanian (Folkestone), end view.
Fig.6, UCL Neg. 2061/29, Cenomanian (Folkestone), oblique view.

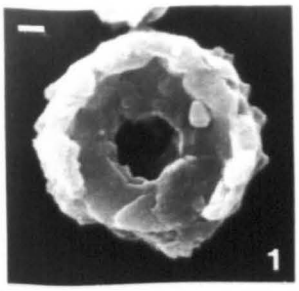
Fig. 7 (a-c): ***Farhania varolii.***
Fig.7a, UCL Neg. 4067/3, Heslerton Borehole, BH-2(67), end view.
Fig.7b, UCL Neg. 4067/6, same specimen (tilted).
Fig.7c, UCL Neg. 4067/7, same specimen (side view).

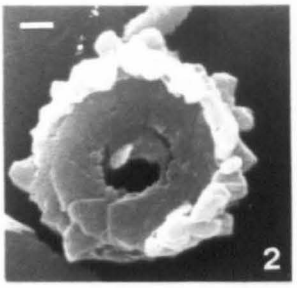
Fig. 8: **Central diaphragm of *Farhania varolii.***
UCL Neg. 4067/1, Heslerton Borehole, BH-2(67).

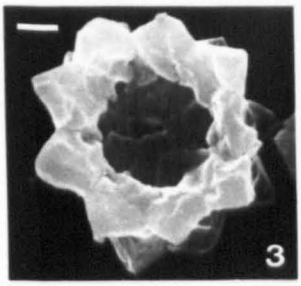
Figs. 9-13: ***Tegulalithus septentrionalis* var.A.**
Fig.9, UCL Neg. 4060/18, Borehole 81/43, 41.16m, end view.
Fig.10, UCL Neg. 4061/9, Borehole 81/43, 41.16m, side and end views.
Fig.11, UCL Neg. 4060/19, Borehole 81/43, 41.16m, side view.
Fig.12, UCL Neg. 4060/23, Borehole 81/43, 41.16m, end view.
Fig.13, UCL Neg. 4063/25, Borehole 81/43, 41.16m, oblique side view.

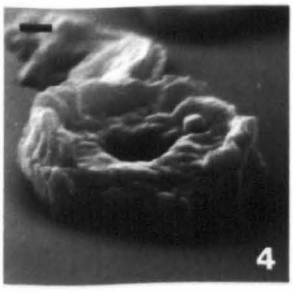
Figs. 14-15: ***Tegulalithus septentrionalis* var.B.**
Fig.14a, UCL Neg. 4070/21, Borehole 81/43, 41.16m, end view.
Fig.14b, UCL Neg. 4070/20, same specimen (tilted).
Fig.15, UCL Neg. 4063/19, Borehole 81/43, 41.16m, oblique side view.

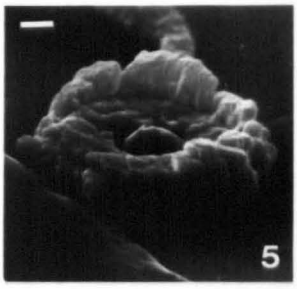
Plate 19

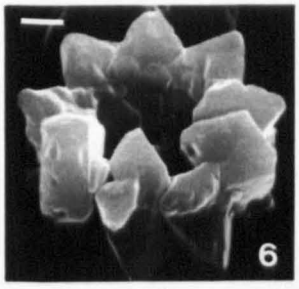

1

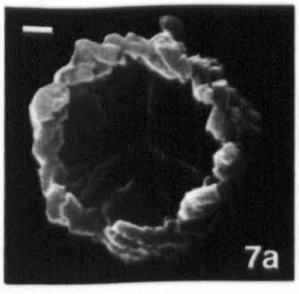

2

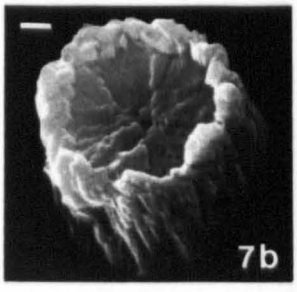

3

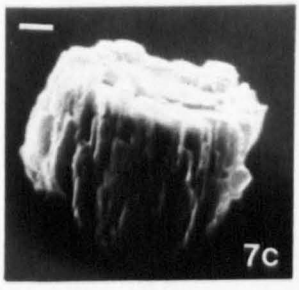

4

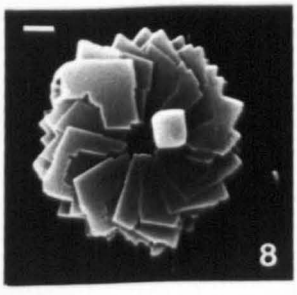

5

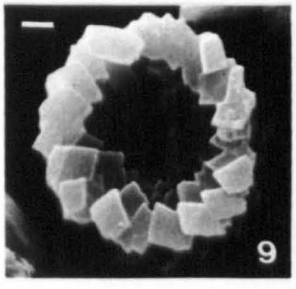

6

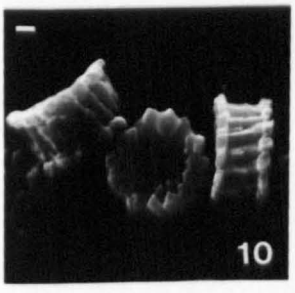

7a

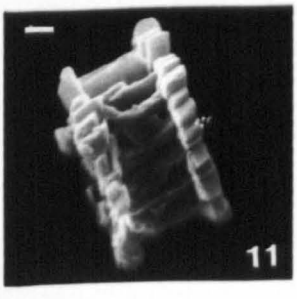

7b

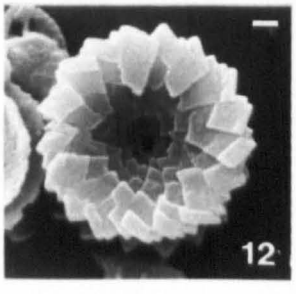

7c

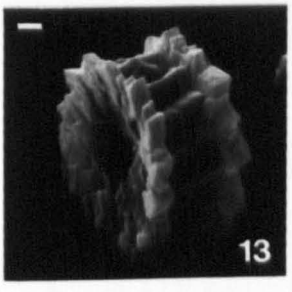

8

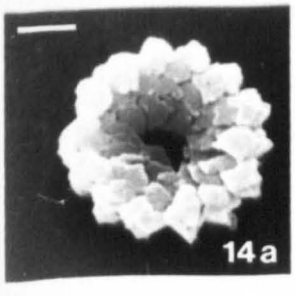

9

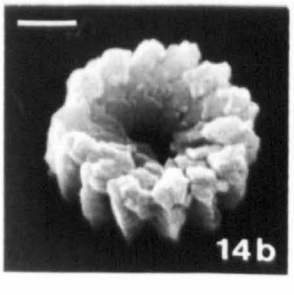

10


11


12


13


14a


14b

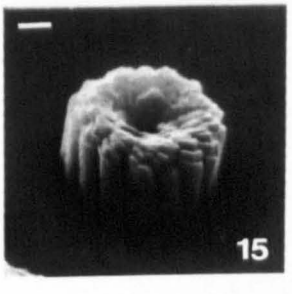

15

PLATE 20

PLATE 20

Polycyclolithaceae and similar forms

Light Micrographs; all at 2000x magnification (scale bar in Fig.18 = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Figs. 1 & 2: ***Radiolithus antiquus.***
Fig.1, UCL Neg. 4021/3; Borehole 81/43, 63.02m; XP.
Fig.2a, UCL Neg. 4074/9; Borehole 81/43, 63.02m; Ph.
Fig.2b, UCL Neg. 4074/7; same specimen in XP - note clear central perforation, and irregularly-formed wall elements.

Figs. 3-6: ***Farhania varolii.***
Fig.3a, UCL Neg. 4074/10, Heslerton Borehole, BH-2(67); XP.
Fig.3b, UCL Neg. 4074/11; same specimen in Ph.
Fig.4a, UCL Neg. 4074/20, Heslerton Borehole BH-2(67); XP.
Fig.4b, UCL Neg. 4974/21, same specimen in Ph.
Fig.5, UCL Neg. 4074/13, Heslerton Borehole, BH-2(67); XP.
Fig.6a, UCL Neg. 4074/14, Heslerton Borehole, BH-2(67); XP (side view).
Fig.6b, UCL Neg. 4074/16, same specimen in Ph.

Figs. 7 & 8: ***Radiolithus planus.***
Fig.7a, UCL Neg. 4074/31, Heslerton Borehole, BH-2(85); XP.
Fig.7b, UCL Neg. 4074/32; same specimen in Ph.
Fig.8, UCL Neg. 5012/12, Heslerton Borehole, BH-2(63); XP.

Figs. 9 & 10: ***Eprolithus floralis.***
Fig.9, UCL Neg. 4089/29, Gault Clay (Folkestone), Bed VII (upper); XP.
Fig.10, UCL Neg. 4094/7, Gault Clay (Folkestone), Bed VII (upper); XP (side view).

Figs. 11-13: ***Tegulalithus septentrionalis* var.A.**
Fig.11, UCL Neg. 4023/27, Borehole 81/43, 41.16m; XP; A = side view; B & C are end views (marginal flange is arrowed on B).
Fig.12, UCL Neg. 4023/23, Borehole 81/43, 41.16m; XP; A = side view; B = end view (with marginal flange arrowed).
Fig.13, UCL Neg. 4023/3, Borehole 81/43, 41.16m; Ph (mid focus - flange not visible).

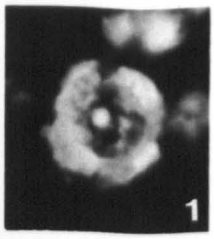
Fig. 14 (a & b): ***Tegulalithus septentrionalis* var.B.**
Fig.14a, UCL Neg. 5012/36; Borehole 81/43, 45.01m; Ph.
Fig.14b, UCL Neg. 5012/35; same specimen in XP - note central perforation, regularly scalloped margin ("bumps" = wall elements) and absence of any marginal flange.

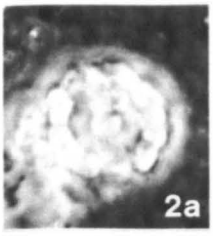
Figs. 15 & 16: ***Rucinolithus windleyae.***
Fig.15, UCL Neg. 4074/24, Borehole 81/43, 41.16m; XP.
Fig.16, UCL Neg.4023/25, Borehole 81/43, 41.16m, XP.

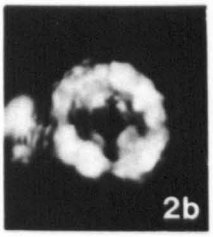
Fig. 17 (a & b): ***Assipetra terebrodentarius.***
Fig.17a, UCL Neg. 4071//11, Borehole 81/43, 11.92m; XP.
Fig.17b, UCL Neg. 4071/12; same specimen in Ph.

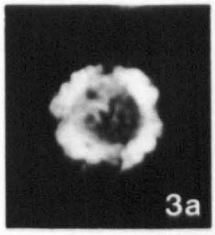
Fig. 18: ***Assipetra infracretacea.***
UCL Neg. 4071/6, Borehole 81/43, 62.38m; XP.

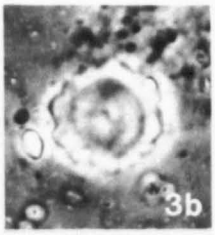
Plate 20

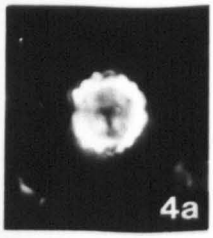

1

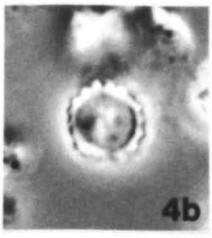

2a

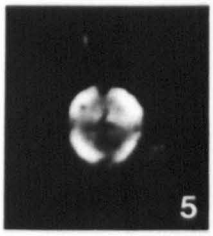

2b

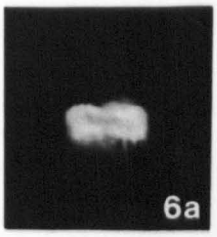

3a

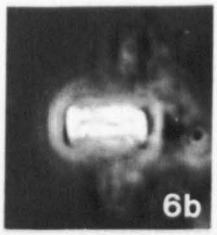

3b

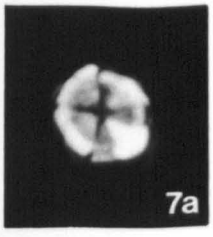

4a

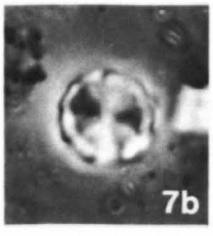

4b

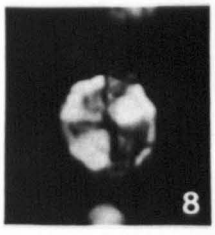

5

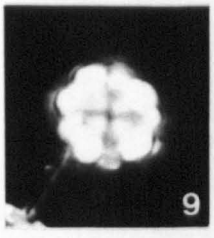

6a

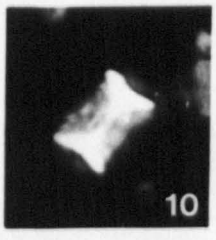

6b

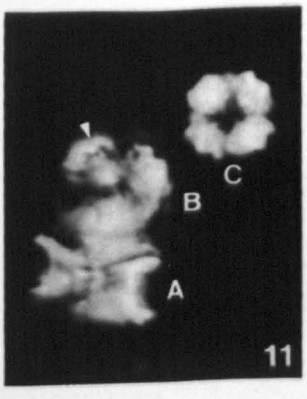

7a

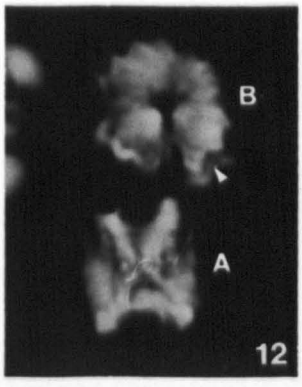

7b

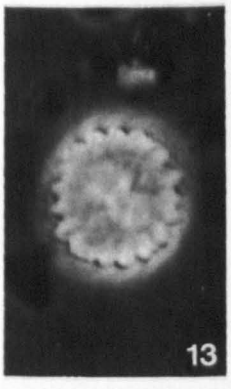

8

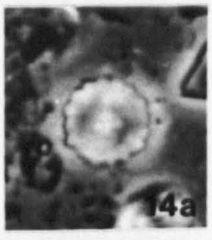

9

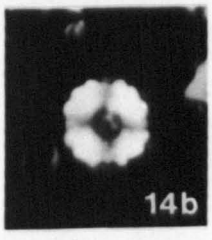

10

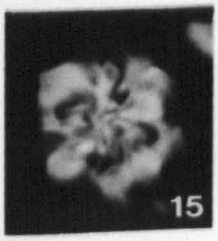

C
B
A
11

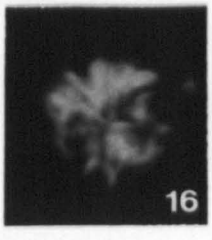

B
A
12

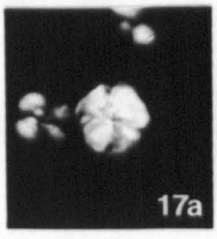

13

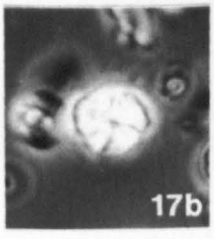

14a


14b


15


16


17a


17b

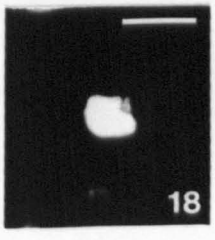

18

PLATE 21

PLATE 21

Scale bar at the top of each SEM = 1μm.

All light micrographs (LMs) are at 2000x magnification (scale bar in Fig.8a = 5μm).
XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Figs. 1-8: ***Rucinolithus windleyae*** **(sp. nov.).**

SEMs:
Fig.1a, UCL Neg. 4063/28, Borehole 81/43, 41.16m, oblique view, **holotype.**
Fig.1b, UCL Neg. 4063/29, same specimen (tilted).
Fig.1c, UCL Neg. 4063/30, same specimen (tilted).
Fig.2, UCL Neg. 4063/31, Borehole 81/43, 41.16m, ?distal view.
Fig.3, UCL Neg. 4063/23, Borehole 81/43, 41.16m, ?distal view.
Fig.4, UCL Neg. 4060/30, Borehole 81/43, 41.16m, side view, **isotype.**

LMs:
Fig.5, UCL Neg. 4074/24, Borehole 81/43, 41.16m; XP.
Fig.6, UCL Neg. 4023/32, Borehole 81/43, 41.16m; XP.
Fig.7, UCL Neg. 4023/24, Borehole 81/43, 41.16m; XP.
Fig.8a, UCL Neg. 4023/11, Borehole 81/43, 41.16m; XP, side view.
Fig.8b, UCL Neg. 4023/13; same specimen in Ph.

Figs. 9-11: ***Assipetra terebrodentarius***.

SEM:
Fig. 9, UCL Neg. 4079/2, Borehole 81/43, 12.79m.

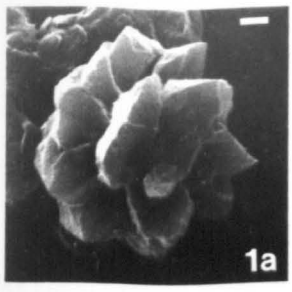
LMs:
Fig.10a, UCL Neg. 4071/17, Borehole 81/43, 11.92m; XP.
Fig.10b, UCL Neg. 4071/18; same specimen in Ph.
Fig.11a, UCL Neg. 4071/13, Borehole 81/43, 11.92m; XP.
Fig.11b, UCL Neg. 4071/14; same specimen in Ph.

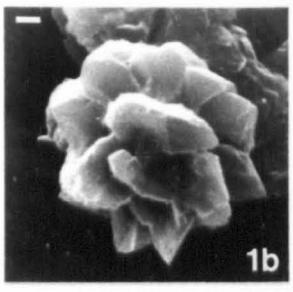
Figs. 12-14: ***Assipetra infracretacea***.

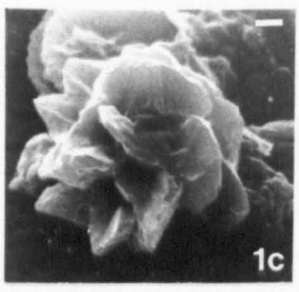
SEM:
Fig.12, UCL Neg. 4068/2, Borehole 81/43, 62.38m.

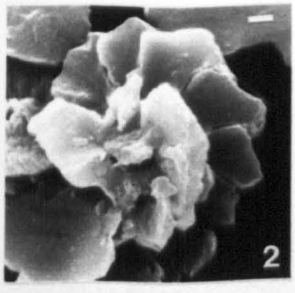
LMs:
Fig.13a, UCL Neg. 4071/2, Borehole 81/43, 62.38m; XP.
Fig.13b, UCL Neg. 4071/3; same specimen in Ph.
Fig.14a, UCL Neg. 4071/4, Borehole 81/43, 62.38m; XP.
Fig.14b, UCL Neg. 4071/5; same specimens in Ph.

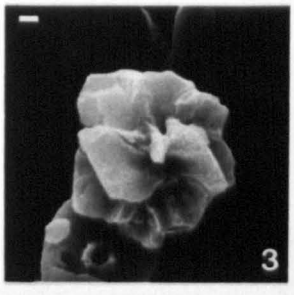
Plate 21

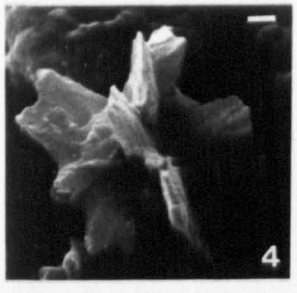

1a

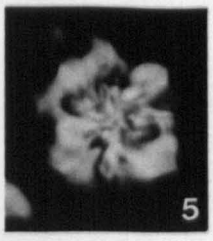

1b

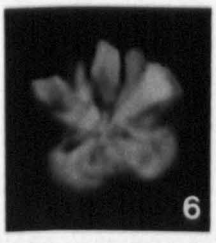

1c


2

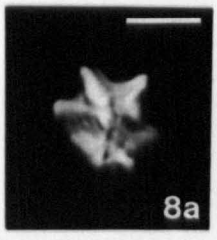

3

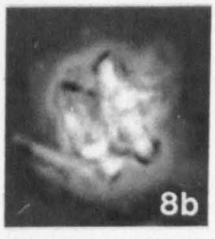

4

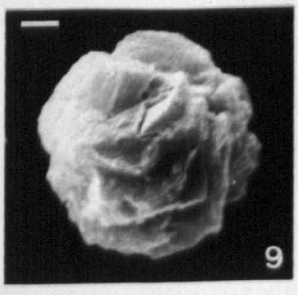

5

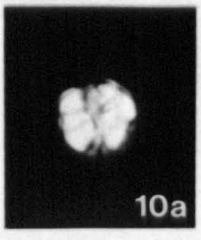

6

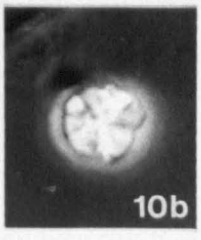

7

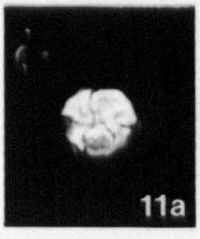

8a

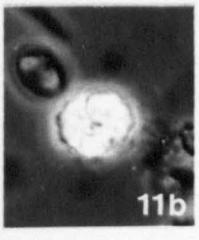

8b

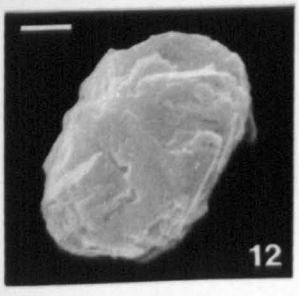

9

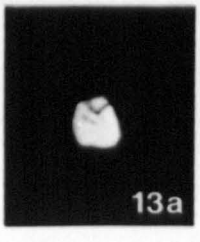

10a

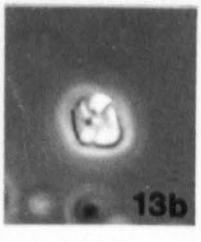

10b

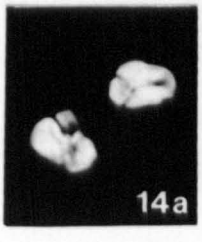

11a


11b


12


13a


13b


14a

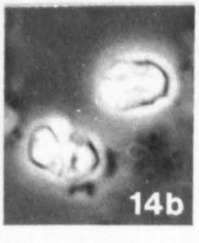

14b

PLATE 22

PLATE 22

***Nannoconus abundans* group**

Scanning Electron Micrographs; scale bar at the top of each micrograph = 1μm.

Figs. 1-5: ***Nannoconus borealis* var.B.**
Fig.1, UCL Neg. 4069/20, Speeton, Bed LB1F (13), side view.
Fig.2, UCL Neg. 4069/21, Speeton, Bed LB1F (13), side view.
Fig.3, UCL Neg. 4069/31, Speeton, Bed LB1F (13), antapical view.
Fig.4, UCL Neg. 4069/24, Speeton, Bed LB1F (13), side view.
Fig.5, UCL Neg. 4069/25, Speeton, Bed LB1F (13), incomplete specimen.

Fig. 6: ***Nannoconus* aff. *borealis*.**
UCL Neg. 4069/30, Speeton, Bed LB1F (13), side view.

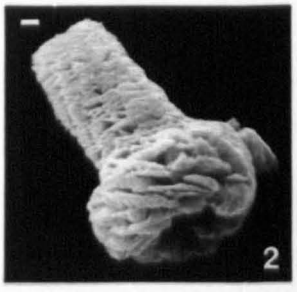
Fig. 7 (a & b): ***Nannoconus borealis* var.A.**
Fig.7a, UCL Neg. 4069/26, Speeton, Bed LB1F (13), oblique side view.
Fig.7b, UCL Neg. 4069/27, same specimen in side view.

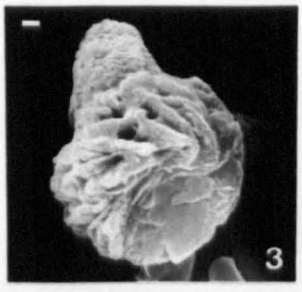
Figs. 8-11: ***Nannoconus abundans*.**
Fig.8, UCL Neg. 3712/3, Speeton, Bed LB1F (13), side view.
Fig.9, UCL Neg. 4069/22, Speeton, Bed LB1F (13), oblique antapical view.
Fig.10, UCL Neg. 4069/23, Speeton, Bed LBIF (13), oblique antapical view.
Fig.11, UCL Neg. 4069/29, Speeton, Bed LB1F (13), side view.

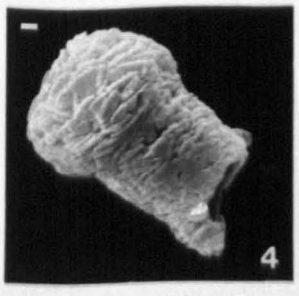
Figs. 12-16: ***Nannoconus inornatus* (sp. nov.).**
Fig.12, UCL Neg. 4079/17, Borehole 81/43, 14.70m, oblique view, **holotype**.
Fig.13, UCL Neg. 4079/16, Borehole 81/43, 14.70m, oblique view.
Fig.14, UCL Neg. 4079/24, Borehole 81/43, 14.70m, oblique view.
Fig.15, UCL Neg. 4079/11, Borehole 81/43, 14.70m, oblique view.
Fig.16a, UCL Neg. 4079/22, Borehole 81/43, 14.70m, oblique view, **isotype**.
Fig.16b, UCL Neg. 4079/21, end view of same specimen.

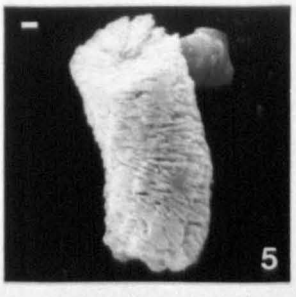
Plate 22

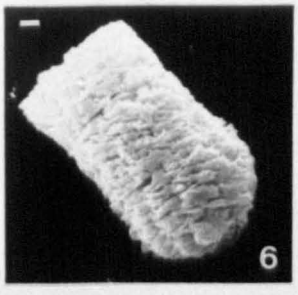

1

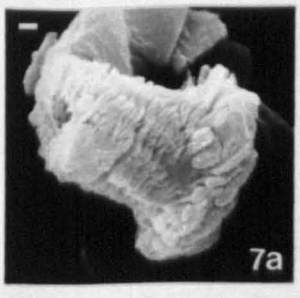

2

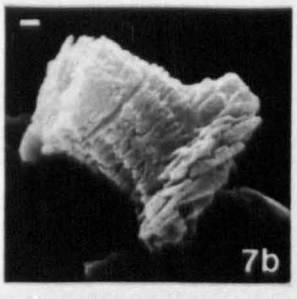

3

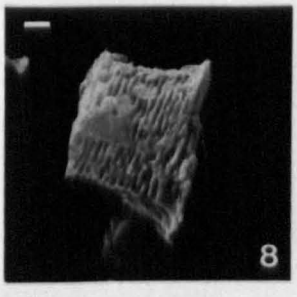

4

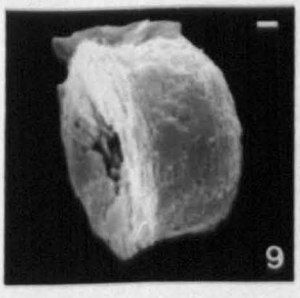

5

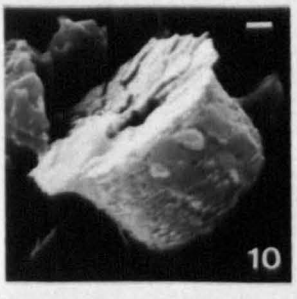

6

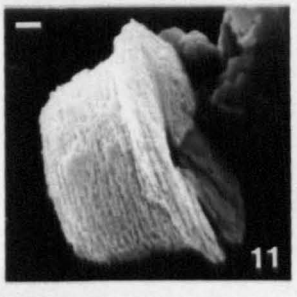

7a

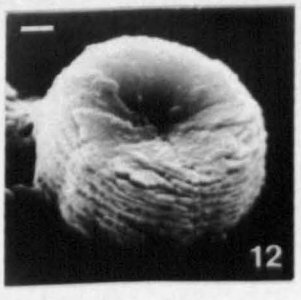

7b

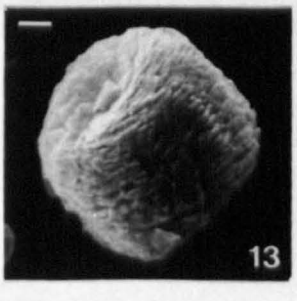

8

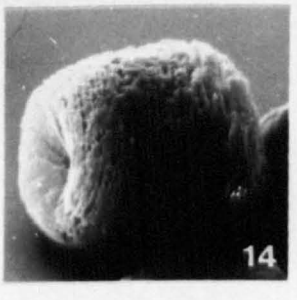

9

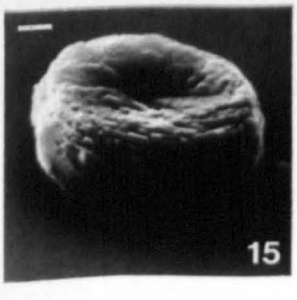

10

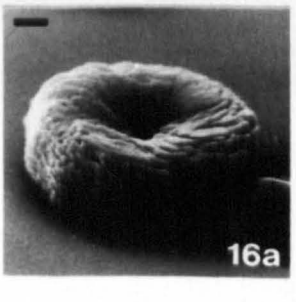

11


12


13


14


15


16a

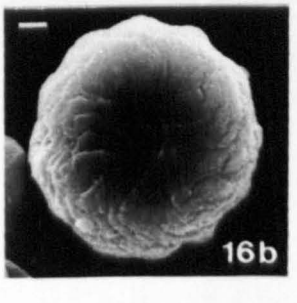

16b

PLATE 23

PLATE 23

Nannoconus

Light Micrographs; all at 2000x magnification (scale bar in Fig.4 = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Figs. 1-4: ***Nannoconus inornatus*** **(sp. nov.).**
Fig.1, UCL Neg. 3545/28, Speeton, Bed LB1F (10); XP (end view).
Fig.2, UCL Neg. 4099/4, Speeton, Bed LB5C.III; XP (side view).
Fig.3a, UCL Neg. 4099/6, Speeton, Bed LB5C.III; XP (end view & side view).
Fig.3b, UCL Neg. 4099/7; same specimens in Ph.
Fig.4, UCL Neg. 3723/11, Speeton, Speeton, Bed LB5C.III; Ph (end views).

Figs. 5-8: ***Nannoconus abundans.***
Fig.5a, UCL Neg. 3545/19; Speeton, Bed LB1F (13); Ph (side view; rudimentary flanged form).
Fig.5b, UCL Neg. 3545/18; same specimen in XP.
Fig.6, UCL Neg. 3545/4, Speeton, Bed LB1F (13); XP (side view).
Fig.7, UCL Neg. 3545/26, Speeton, Bed LB1F (10); XP (end view).
Fig.8, UCL Neg. 3545/34, Speeton, Bed LB1F (7); XP (end view; wide flanged variety).

Figs. 9 & 10: ***Nannoconus borealis*** **var. A.**
Fig.9, UCL Neg. 3545/9, Speeton, Bed LB1F (13); Ph (side view).
Fig.10, UCL Neg. 3545/6, Speeton, Bed LB1F (13); XP (side view).

Figs. 11 & 12: ***Nannoconus borealis*** **var.B (fully developed).**
Fig.11, UCL Neg. 3545/2, Speeton, Bed LB1F (13); XP (side view; slightly oblique).
Fig.12, UCL Neg. 3545/20, Speeton, Bed LB1F (13); XP (end view; partial specimen).

Fig. 13: ***Nannoconus abundans*** **(isolated flange).**
UCL Neg. 3545/32, Speeton, Bed LB1F (7); XP.

Figs. 14 & 15: ***Nannoconus pseudoseptentrionalis*** **(sp. nov.).**
Fig.14a, UCL Neg. 4094/20, Speeton, Lower Cement Bed 49; XP.
Fig.14b, UCL Neg. 4094/21; same specimen in Ph.
Fig.15, UCL Neg. 4065/32, Speeton, Lower Cement Bed 49; XP.

Figs. 16 & 17: ***Nannoconus globulus.***
Fig.16, UCL Neg. 5012/21, Borehole 81/43, 64.79m; XP (end view).
Fig.17, UCL Neg. 5012/22, Borehole 81/43, 64.79m; XP (side view).

Figs. 18 & 19: ***Nannoconus kamptneri.***
Fig.18, UCL Neg. 5005/8, Speeton, Bed C9C (28); XP (side view).
Fig.19, UCL Neg. 4099/11, Borehole 81/43, 31.76m; XP (slightly oblique side view).

Figs. 20: ***Nannoconus truitti truitti.***
UCL Neg. 5012/23, Sutterby Marl, 146'1"; XP (side view).

Fig. 21: ***Nannoconus truitti frequens.***
UCL Neg. 5012/25, Sutterby Marl, 146'1"; XP (side view).

Plate 23

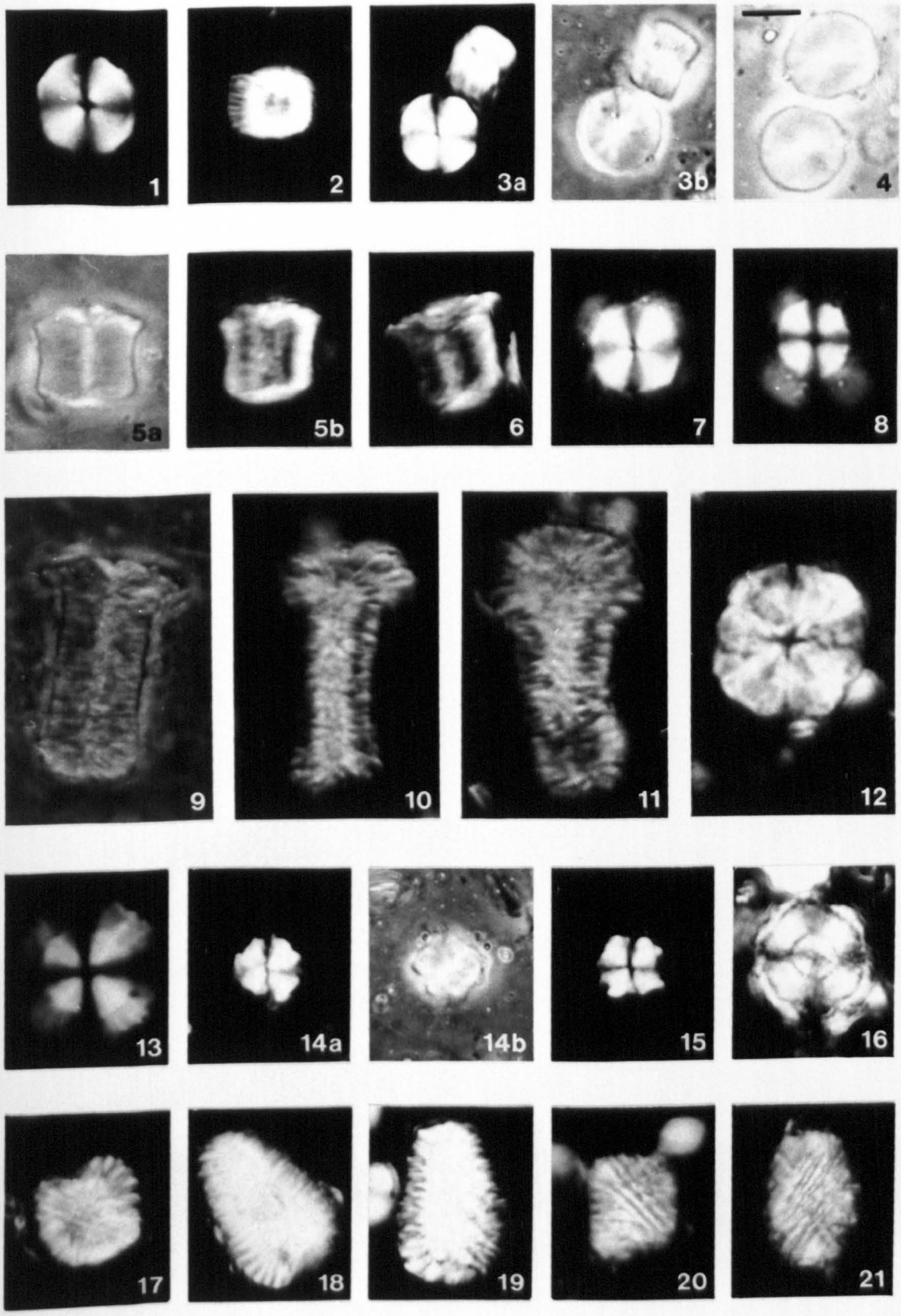


PLATE 24

PLATE 24

Scanning Electron Micrographs.
Scale bars in Figs.1-5 = 5μm.
Scale bars in Figs.6-7 = 1μm.

Figs. 1-5: **Sediment surface SEMs (Speeton, Bed LB1F (sample 13)).**

Figs.1 & 2: ***Nannoconus abundans.***
Fig.1, UCL Neg. 3815/4.
Fig.2, UCL Neg. 3814/32.

Fig.3: ***Nannoconus abundans*** **(A),** ***Nannoconus borealis*** **var.A (B), & pyritic spherule (C).**
UCL Neg. 3814/33.

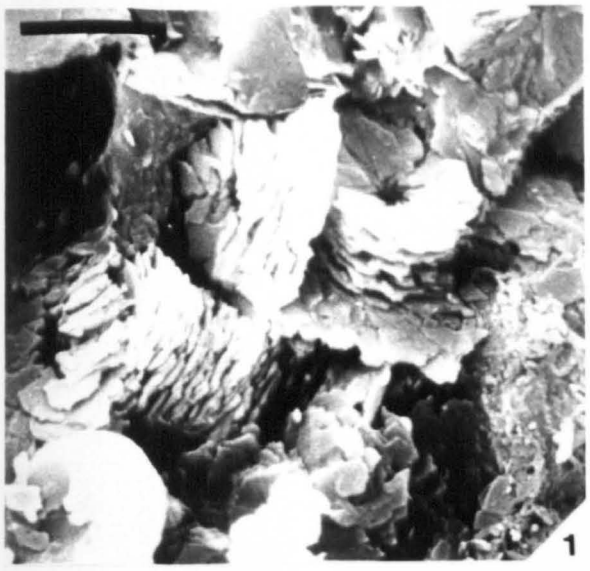
Fig.4: ***Nannoconus borealis*** **var.A** (several specimens).
UCL Neg. 3814/35.

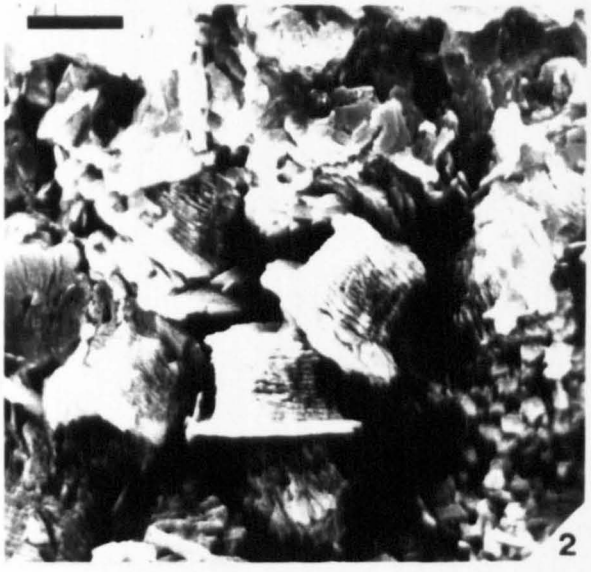
Fig.5: **Nannoconid and coccolith covered surface.**
UCL Neg. 3814/28.

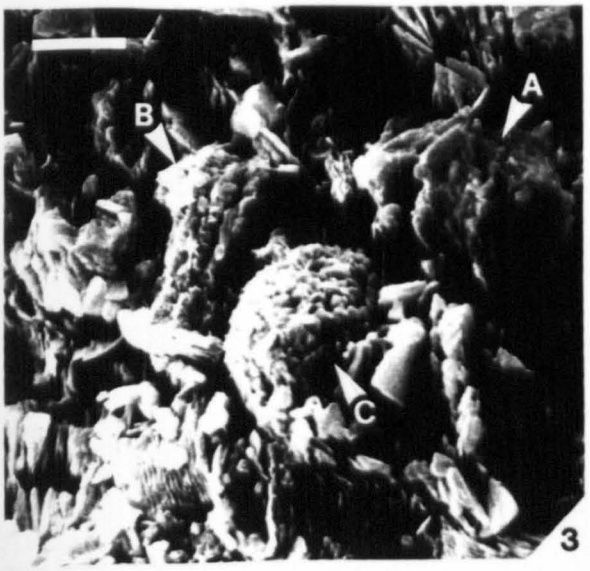
Figs. 6 & 7: ***Nannoconus*** **cf.** ***N.inornatus.***

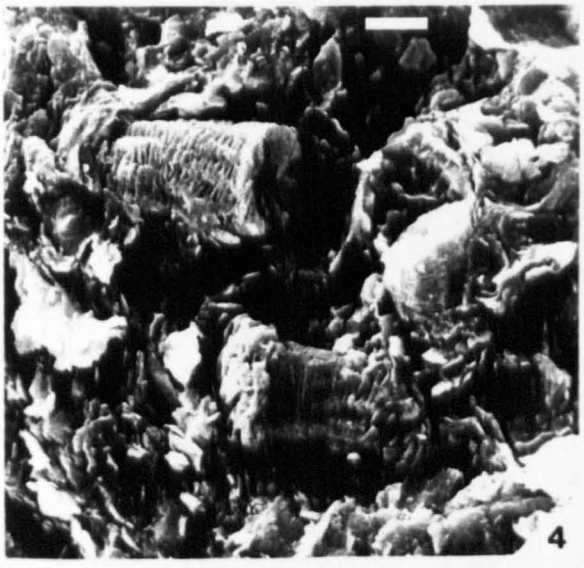
Fig.6a, UCL Neg. 4079/25, Borehole 81/43, 14.70m, end view.
Fig.6b, UCL Neg. 4079/26, same specimen (tilted).

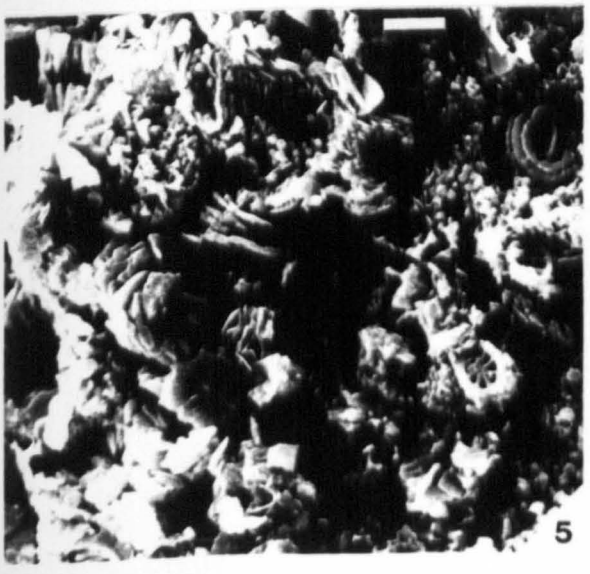
Fig.7a, UCL Neg. 4079/14, Borehole 81/43, 14.70m, end view.
Fig.7b, UCL Neg. 4079/15, same specimen (tilted).

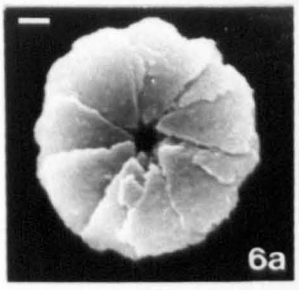

1

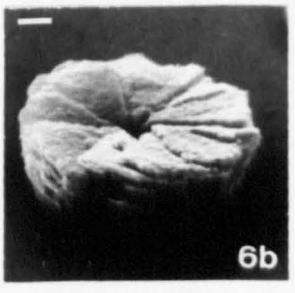

2

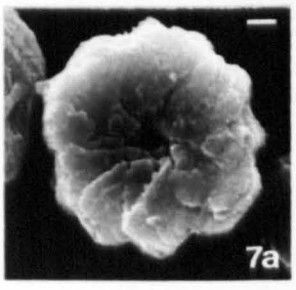

A
B
C
3


4


5


6a


6b


7a

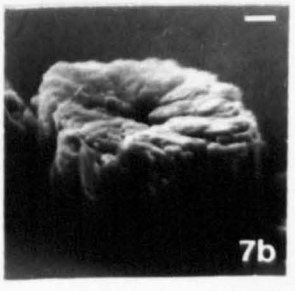

7b

PLATE 25

PLATE 25

Scanning electron Micrographs; scale bar at the top of each micrograph = 1μm.

Figs. 1 & 2: ***Nannoconus globulus.***
Fig.1a, UCL Neg. 4067/29, Borehole 81/43, 31.76m, side view.
Fig.1b, UCL Neg. 4067/28, end view of same specimen.
Fig.2a, UCL Neg. 4061/16, Borehole 81/43, 32.80m, side view.
Fig.2b, UCL Neg. 4061/15, end view of same specimen.

Fig. 3 (a & b): ***Nannoconus* sp. (cf. *N.elongatus*).**
Fig.3a, UCL Neg. 4074/4, Borehole 81/43, 32.80m, side view.
Fig.3b, UCL Neg. 4074/3, end view of same specimen.

Figs. 4-6: ***Nannoconus globulus* (coarsely ribbed variety).**
Fig.4, UCL Neg. 4073/2, Borehole 81/43, 64.79m, oblique view.
Fig.5, UCL Neg. 4073/3, Borehole 81/43, 64.79m, oblique view.
Fig.6, UCL Neg. 4073/19, Borehole 81/43, 64.79m, end view.

Fig. 7: **Nannoconid fragment.**
UCL Neg. 4073/14, Borehole 81/43, 64.79m.

Fig. 8: ***Nannoconus kamptneri.***
UCL Neg. 4073/26, Borehole 81/43, 64.79m, side view.

Fig. 9: ***Conusphaera rothii.***
UCL Neg. 3264/28, Speeton, Bed D2A, side view (poorly preserved specimen; identity confirmed by transfer from LM).

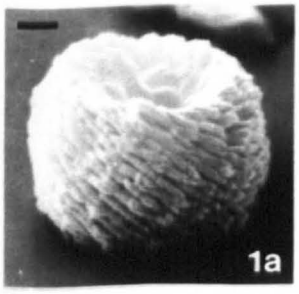
Figs. 10 & 11: ***Micrantholithus obtusus.***
Fig.10, UCL Neg. 4061/4, Borehole 81/43, 41.16m.
Fig.11, UCL Neg. 3264/26, Speeton, Bed D2A, single segment (1/5th).

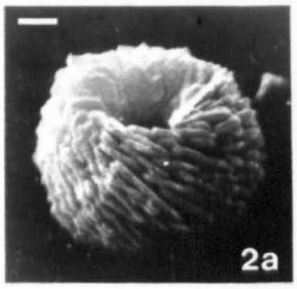
Fig. 12: ***Micrantholithus hoschulzii.***
UCL Neg. 4079/19, Borehole 81/43, 14.70m.

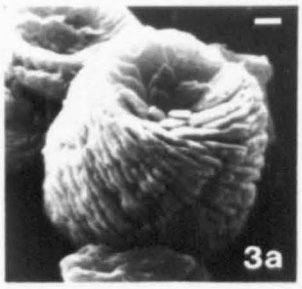
Figs. 13 & 14: ***Rhabdophidites parallelus.***
Fig. 13, UCL Neg. 3815/2, Speeton, Bed LB1F (13), collapsed coccosphere.
Fig.14, UCL Neg. 3814/12, Speeton, Bed C2E (30), side view.

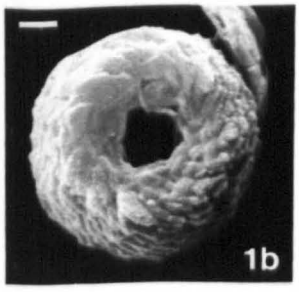
Fig. 15: ***Lithraphidites carniolensis*** (with 'skewered' *Apertasphaera jakubowskii*).
UCL Neg. 4068/9, Borehole 81/43, 18.00m.

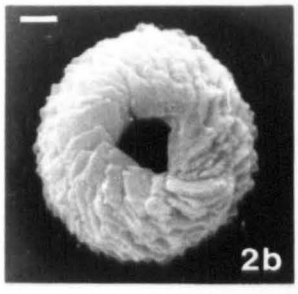
Plate 25

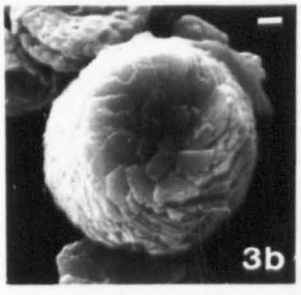

1a

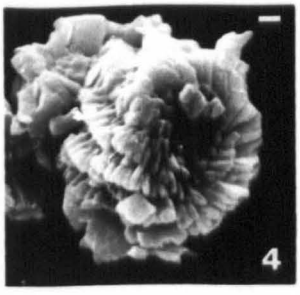

2a

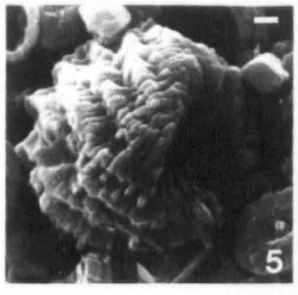

3a

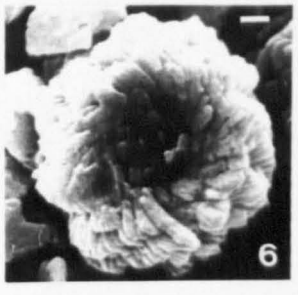

1b

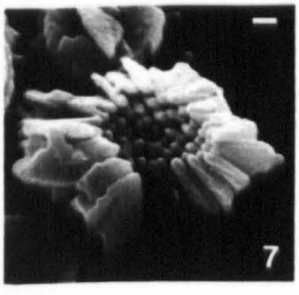

2b

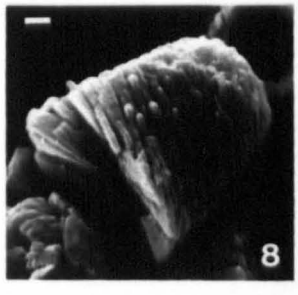

3b

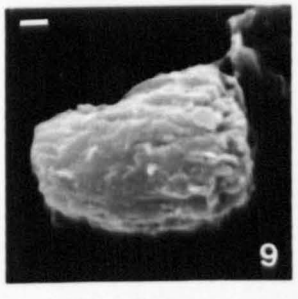

4

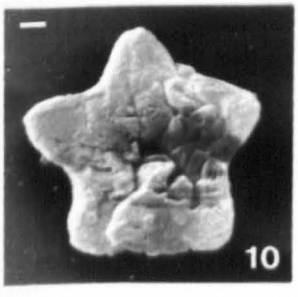

5

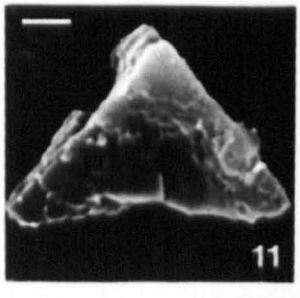

6

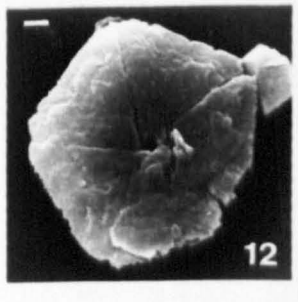

7


8

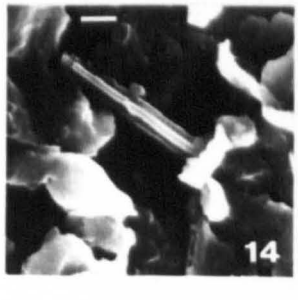

9


10


11


12


13


14

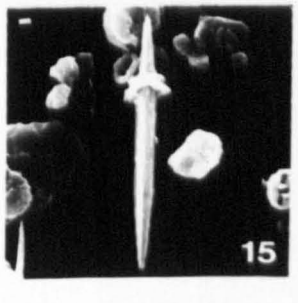

15

PLATE 26

PLATE 26

Light Micrographs; all at 2000x magnification (scale bar in Fig.4 = 5μm).

XP = cross-polarised illumination (polarising directions parallel to length and breadth of the page).
Ph = phase contrast illumination.

Figs. 1-4: ***Micrantholithus speetonensis.***
Fig.1, UCL Neg. 4020/16, Speeton, Bed D3C; XP.
Fig.2, UCL Neg. 5005/1, Speeton, Bed D3A; XP.
Fig.3, UCL Neg. 3697/10, Speeton, Bed D3A; XP, partial specimen (2/5ths).
Fig.4, UCL Neg. 3697/12, Speeton, Bed D3A; XP, partial specimen (1/5th).

Fig. 5: ***Micrantholithus obtusus.***
UCL Neg. 4071/1, Borehole 81/43, 17.00m; XP.

Fig. 6: ***Micrantholithus hoschulzii.***
UCL Neg. 4097/3, Borehole 81/43, 61.36m; XP.

Fig. 7: ***Micrantholithus hoschulzii*** **(A)** **&** ***Lithraphidites bollii*** **(B).**
UCL Neg. 4021/34, Borehole 81/43, 31.76m; XP.

Fig. 8: ***Kokia curvata.***
UCL Neg. 3724/16, Core 7B, 8.00m; XP.

Fig. 9 (a & b): ***Kokia borealis.***
Fig.9a, UCL Neg. 3724/10, Core 7B, 9.90m; XP.
Fig.9b, UCL Neg. 3724/11; same specimen in Ph.

Figs. 10-13: ***Triquetrorhabdulus shetlandensis.***
Fig.10, UCL Neg. 4019/12, Speeton, Bed D3C; XP.
Fig.11, UCL Neg. 4019/15, Speeton, Bed D3C; XP.
Fig.12, UCL Neg. 4019/16, Speeton, Bed D4A; XP (note serrate blade margin).
Fig.13, UCL Neg. 4019/10, Borehole 81/43, 66.28m; XP (group of 3 small specimens).

Fig. 14: ***Ceratolithina cruxii.***
UCL Neg. 4089/31, Gault Clay (Folkestone), Bed VII (upper); XP.

Fig. 15: ***Ceratolithina hamata.***
UCL Neg. 4089/17, Gault Clay (Folkestone), Bed VII (upper); XP.

Fig. 16: ***Ceratolithina bicornuta.***
UCL Neg. 4095/12, Gault Clay (Folkestone), Bed VII (upper); XP.

Plate 26

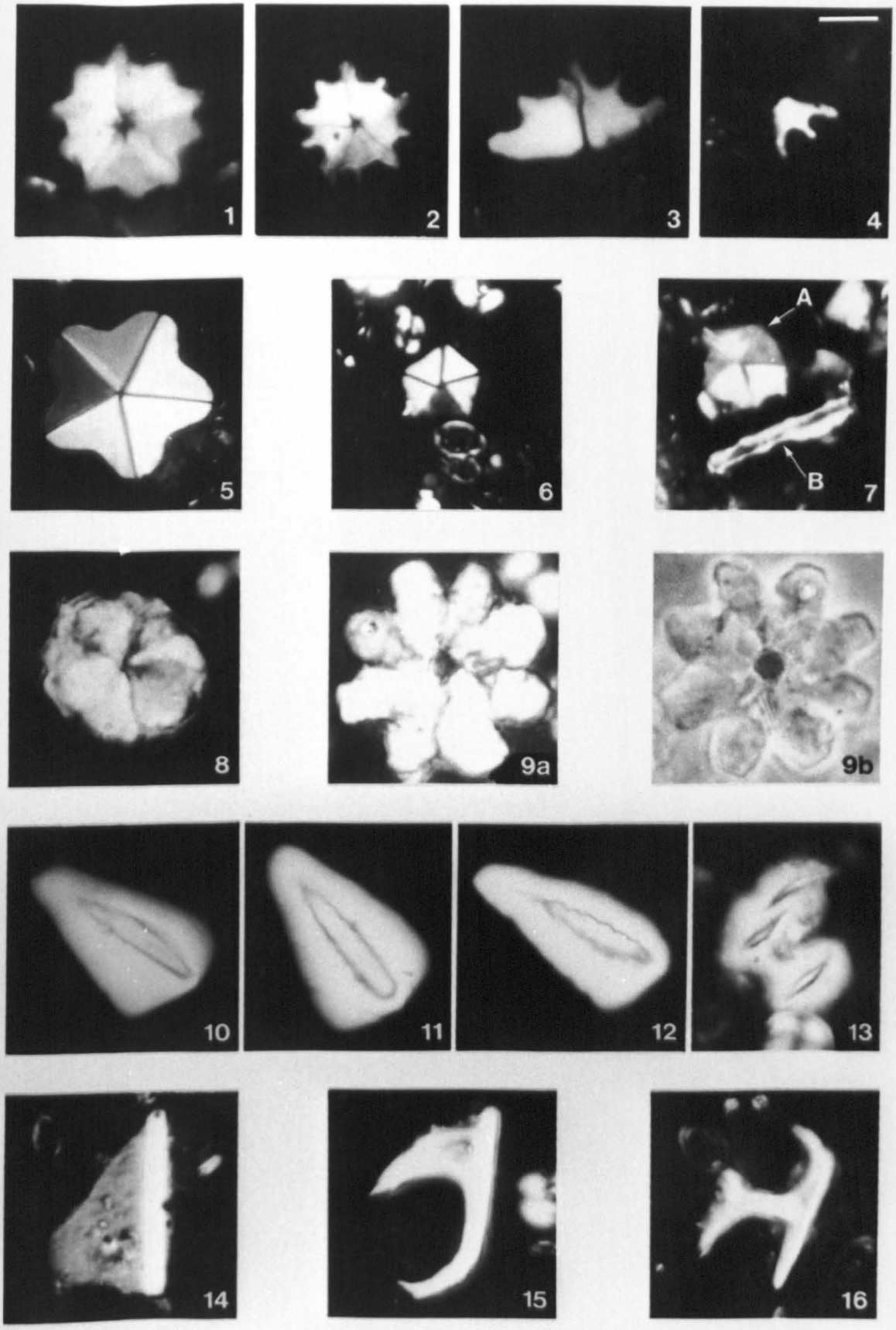


PLATE 27

PLATE 27

Spicular nannofossils

Scale bar at the top of each SEM = 5μm.

All light micrographs (LMs) were taken in cross-polarised light, at 2000x magnification (scale bar in Fig.4 = 5μm).

Figs. 1-4: ***Micrascidites?* sp.**

Fig.1 (SEM), UCL Neg. 4060/15, Borehole 81/43, 90.45m; note abundance of fusiform spicules (Wb = *Watznaueria britannica*; Cm = *Cyclagelosphaera margerelii*).
Fig.2 (SEM), UCL Neg. 4060/14, Borehole 81/43, 90.45m.
Fig.3 (SEM), UCL Neg. 4060/13, Borehole 81/43, 90.45m.
Fig.4 (LM), UCL Neg. 4065/2, Borehole 81/43, 90.45m.

Figs. 5-7: ***Monniotia?* sp.**
Fig.5 (SEM), UCL Neg. 4073/35, Borehole 81/43, 32.80m.
Fig.6 (LM), UCL Neg. 4099/13, Borehole 81/43, 28.77m.
Fig.7 (LM), UCL Neg. 4099/12, Borehole 81/43, 28.77m.

Fig. 8 (LMs): **Spicule sp.1.**
UCL Neg. 4019/27, Borehole 81/43, 29.37m; XP.

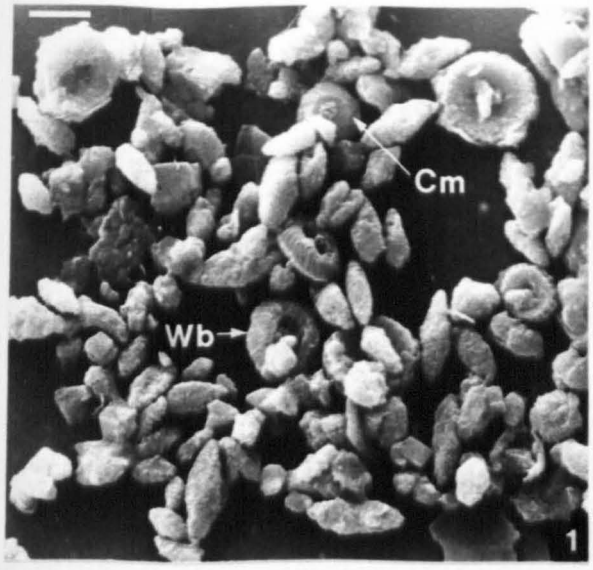
Figs. 9 & 10 (LMs): **Spicule sp.2.**
Fig.9, UCL Neg. 4019/25, Borehole 81/43, 30.24m; XP.
Fig.10, UCL Neg. 4019/17, Borehole 81/43, 58.72m; XP.

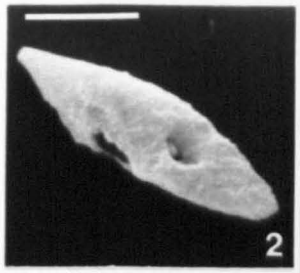
Figs. 11 & 12 (LMs): ***Triquetrorhabdulus?* sp.1.**
Fig.11, UCL Neg. 4023/20, Borehole 81/43, 41.16m; XP.
Fig.12, UCL Neg. 5015/5, Borehole 81/43, 45.80m; XP.

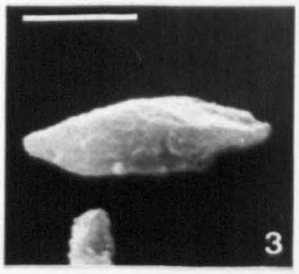
Figs. 13 & 14 (SEMs): ***?Triquetrorhabdulus?* sp.1.**
(LM-SEM specimen transfer required)
Fig.13 (SEM), UCL Neg. 4060/37, Borehole 81/43, 41.16m.
Fig.14 (SEM), UCL Neg. 4061/1, same specimen.

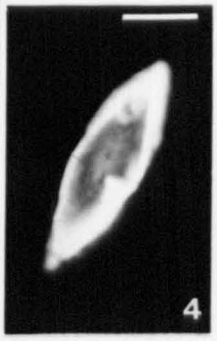
Fig. 15 (SEM): ***?Triquetrorhabdulus shetlandensis.***
(LM-SEM specimen transfer required)
UCL Neg. 4069/33, Borehole 81/43, 63.99m.

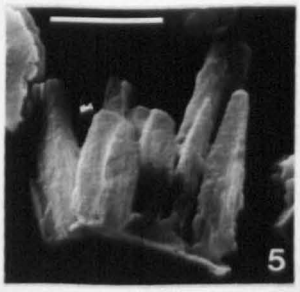
Plate 27

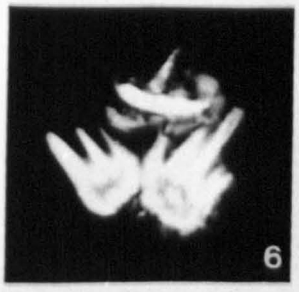


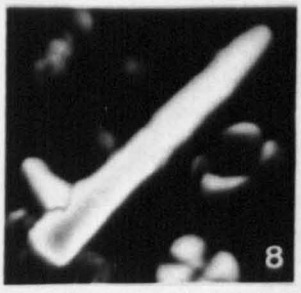


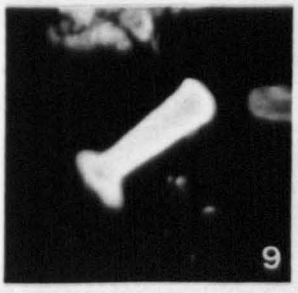


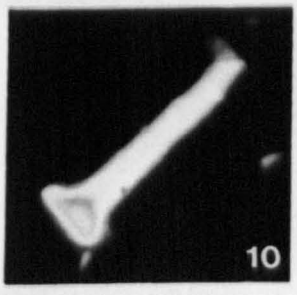


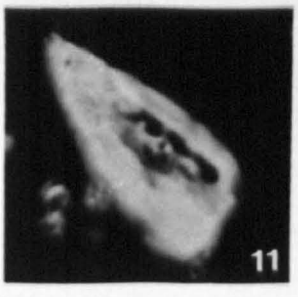


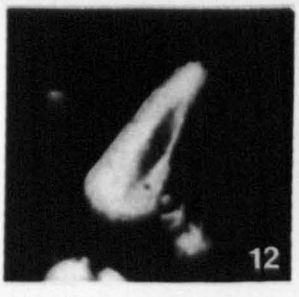


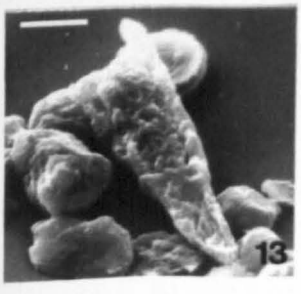


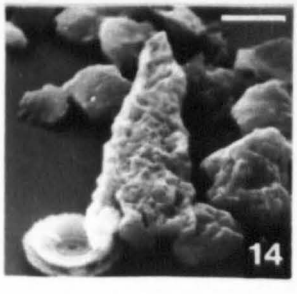


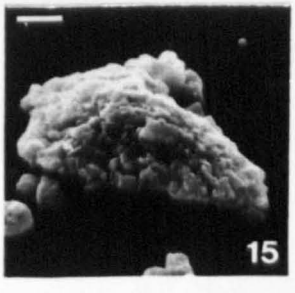












CHAPTER 3 - BIOSTRATIGRAPHY

3.1 - INTRODUCTION

The following terms and abbreviations are used throughout this chapter:

First Occurrence (FO) = lowest occurrence, first appearance or "base", but does not necessarily represent the evolutionary origination of the species in question, since species may have diachronous **First Occurrence Datums (FODs)**.

Last Occurrence (LO) = highest occurrence, "top" or first downhole occurrence; again this does not necessarily imply the evolutionary extinction of the species in question, since **Last Occurrence Datums (LODs)** may be diachronous.

Continuity of Range (COR) - The continuity, or consistency of range is a major factor when selecting marker species. Following Bergen (1994) the COR of potential marker species are quantified using the percentage of **nannofossiliferous samples (sa)** in which a species was recorded throughout its entire stratigraphical range, e.g. COR = 90% (100 sa) indicates that a species was recorded in 90 out of 100 consecutive samples. Similarly, the reliability of first and last occurrence datums are indicated by the records from the **bottom (B)** and **top (T)** ten (where possible) nannofossiliferous samples of a species' range, e.g. T 9/10 sa indicates that a species was recorded in 9 out of 10 consecutive samples below its LOD. The COR is largely dependant on the time spent logging slides; it is difficult to be entirely objective but, in this study, at least 80 minutes (inclusive of counting time) were spent on each slide. The results obtained should thus be almost reproducible under industrial conditions; they are not, however, so thorough that they cannot be refined. Despite this fairly thorough logging, a number of species that have previously been used as markers in the Boreal area were observed to have very discontinuous ranges (e.g. *Conusphaera rothii*, *Cruciellipsis cuvillieri*, *Speetonia colligata*). These species are not used as zonal markers, but remain useful secondary markers, and may be useful in inter-regional correlation. An ideal marker species should be large, robust and common/abundant throughout a continuous range; several species fulfil these criteria admirably in the Boreal area (e.g. *Tegulalithus septentrionalis* and *Eiffellithus striatus*). A number of species have a low overall COR but occur very consistently throughout certain extended intervals, often just prior to their LOs (e.g. *Clepsilithus maculosus*, *Rhagodiscus pseudoangustus*); it is uncertain whether these LOs represent true extinction events, but these species remain valuable markers.

Abundance Categories - Abundance estimates vary greatly among authors, and it is thus essential that any category is accurately defined. The following abundance categories are defined in terms of a variety of easily assessed criteria, of varying reliability. The most easily assessed accurate criterion is the number of specimens per standard (300+)

count; this can be quickly assessed in well-preserved material, does not involve any calculation, and is thus well-suited to realistic, well-site/shipboard reproducibility. Percentage abundance figures (% of assemblage) are obviously more reliable, since the "standard" 300+ counts are not, in fact, standard (300-400 specimens were generally counted), but these involve some numerical calculation. The most commonly used but least reproducible means of estimating nannofossil abundance is by the "number of specimens per field of view". This is largely dependant on the thickness of the slide and the amount of dilution by detrital material. Nevertheless, this rough means of abundance estimation retains some utility, and the abundance categories used herein are also qualified in terms of the # / mean FOV (it is assumed that nannofossil preservation is good, and that slides are of "average" thickness, yielding roughly 50 nannofossils per field of view at a magnification of 1,250x).

	# / 300+ count	% of assemblage	# / mean FOV
Rare	0	-	-
Few	0	<0.3%	-
Common	1-5	c.1%	<1
Abundant	6-60	2-20%	>1
Very Abundant	>60	>20%	>10

Rare indicates that a single specimen was recorded during biostratigraphical logging; **Few** indicates that several specimens were recorded outside the standard count.

Acme - Period of exceptional abundance (abundant / very abundant) of a consistently present species. The acmes observed in the Lower Cretaceous are much less dramatic than those used to zone the Quaternary (Weaver & Hine, *in press*) but, nevertheless, a number of species form regionally correlatable acmes that are often more easily identified than the F/LOs of (rare) marker species. These events have low potential for inter-regional correlation but, when utilised in conjunction with discrete F/LODs, they permit much improved resolution within a particular basin. Long-term acmes may be slightly patchy in nature, in that not every sample from the acme interval yields a high relative abundance of the acme-forming species; the continuity of an acme is obviously an important consideration when attempting to use such events for correlation. Graphic plotting of abundance data is not usually necessary for identification of acmes; providing that a reasonably consistent counting technique is applied, regionally correlatable acmes can generally be picked out from basic count data.

Influx - Period during which a species that is otherwise extremely rare or absent is recorded consistently (and perhaps commonly). Influx forming species are known to have longer, continuous ranges elsewhere, and most are clearly Tethyan-derived. Other influxing species (e.g. *Watznaueria britannica*) have more cryptic environmental

preferences. This term is not used in the same sense as other authors (e.g. Jakubowski, 1987; Varol, 1989; Jeremiah, *in press*), who tend to refer to first downhole common/abundant occurrences (= acme tops) as "influxes".

Re-entry - Reappearance of a species after an extended absence from a region (for presumed ecological reasons). *Clepsilithus maculosus* re-entered the North Sea area in dramatic fashion during the Late Hauterivian; this species seems to have retreated to lower latitudes during its (mid-Hauterivian) absence from the region.

Throughout this and the following chapter generic epithets are abbreviated after first introduction; full taxonomic citations may be obtained in section 2.4 (Systematic Palaeontology).

3.2 - PREVIOUS WORK ON LOWER CRETACEOUS NANNOFOSSIL BIOSTRATIGRAPHY

3.2.1- Seminal studies

Early biostratigraphical studies were based on low-latitude, Tethyan sections; Boreal workers (e.g. Black) tended to concentrate on taxonomic subdivision and, although they published some useful distribution data, they did not attempt any division of the geological column into zones. The earliest biostratigraphical studies utilised various species of *Nannoconus* - Bronnimann (1955) and Trejo (1960), recognised a number of distinctive nannoconid assemblages in Cuba and Mexico, respectively. Worsley (1971) published a zonation for the Lower Cretaceous of the Caribbean Sea (DSDP Sites 4 and 5), with six zones spanning the Kimmeridgian to Albian. However, Worsely's zonation was based on only seven samples and utilised a number of obscure species, and has thus been ignored by later workers. Manivit (1971) divided the Aptian-Albian of France into six zones, but the sequence and timing of the her events have been discredited by later studies.

Thierstein (1971) proposed a tentative zonation for the entire Lower Cretaceous, comprising nine zones, and subsequently (1973) supplied validation in the form of detailed range charts. This mammoth study was based on low-latitude material - primarily on the stratotype and parastratotype sections of S.E. France, on a number of Atlantic DSDP Sites, and on sections in Switzerland and South America. Unfortunately Thierstein had only three samples from the Neocomian of Boreal latitudes (from the Hauterivian of Nettleton), and did not realise the extent of nannofloral provincialism. This scheme is also limited by the poor definition of a number of its marker species (notably *Chiastozygus litterarius* and *Rhagodiscus angustus*).

3.2.2 - The development of Boreal nannofossil biostratigraphy

Sissingh (1977) produced a widely utilised nannofossil zonation scheme for the entire Cretaceous. The Neocomian part of this scheme was based on 27 samples from Speeton, and on interpolated data from Thierstein (1973). Thus, Sissingh used a mixed suite of Boreal and Tethyan marker species, but mainly the latter, since he appears to had more faith in Thierstein's data. It follows that, due to the strong provincialism during this interval, none of Sissingh's six Neocomian zones are readily identifiable in the Boreal area, although the scheme is still largely workable at low-latitudes. An additional limitation is that several marker species (*Cretarhabdus loriei* and *Chiastozygus litterarius*) are poorly defined.

Perch-Nielsen (1979) recognised the limited applicability of previous nannofossil zonations in the Boreal area. She used a limited number of samples (25) from Speeton, and knowledge acquired from North Sea studies, to integrate a number of important events with the Tethyan-based schemes of Thierstein (1976) and Sissingh (1977). The most notable of these events (Fig.3.1) are the FO and LO of *Chiastozygus striatus* (= *Eiffellithus striatus*), the FO and LO of *Micrantholithus speetonensis*, and the FO of *Eprolithus antiquus* (= *Radiolithus antiquus*). Unfortunately she misplaced the LO of *R.antiquus*, due to her inclusion of forms now assigned to *Farhania varolii.*

Taylor (1978) conducted the first really comprehensive study of the Speeton section, examining some 95 samples. Based on this and other sections she (1982) proposed 9 nannofossil zones, spanning the Late Ryazanian to Late Albian. The Aptian-Albian part of Taylor's scheme is essentially that of Thierstein (1971, 1973), but she used several apparently endemic Boreal species to subdivide the Neocomian (*C.salebrosum*, *M.speetonensis* and *N.abundans*). Also, significantly, she recorded the FO of *"Dodekapodorhabdus noelii"* (= *Perissocyclus plethotretus/tayloriae*) as a useful event in the Late Hauterivian (later authors have had broader concepts of these species, and thus not identified this event). Like Perch-Nielsen (1979), Taylor used the FO of *"C.striatus"* (= *E.striatus*), but was unable to identify the LO of this species, due to her broader species concept.

Jakubowski (1987) proposed a detailed subdivision of the Lower Cretaceous of the Moray Firth Basin based on offshore well material, with limited outcrop material (from Speeton, Nettleton, and Germany) for calibration against stage limits. Nineteen zones (labelled NLK 1-19, in descending order) spanning the Ryazanian-Albian were defined using LOs (= first downhole occurrences). Significantly, a number of these zones were defined using abundance data (first downhole common/abundant occurrences) rather than the discrete LOs of "marker" species, as traditionally used. A further 11 subzones were

RYAZ.
VALANGINIAN
HAUTERIVIAN
BARREMIAN
APTIAN
ALBIAN
UPPER
LOWER
UPPER
LOWER
UPPER
LOWER
UPPER
LOWER
UPPER
LOWER
MID.
UPPER
PERCH-NIELSEN, 1979
TAYLOR, 1982
JAKUBOWSKI, 1987
THOMSEN, 1987
CRUX, 1989, 1991
MUTTERLOSE, 1991
BRALOWER, 1991
VAROL, 1992
NLK 19
NLK 18
NLK 17
NLK 16
NLK 15
NLK 14
NLK 13
NLK 12
NLK 11
NLK 10
NLK 9
NLK 8
NLK 7
NLK 6
NLK 5
NLK 4
NLK 1-3
TETHYAN TAXA
LODs
FODs
Nannoconus Acmes
FOD
LOD

defined using FOs. No detailed range charts were published, but this study still represents the most complete published account of the offshore (expanded) Lower Cretaceous, and the general sequence of LODs remains irrefutable.

Thomsen (1987) conducted a thorough study on four wells in the Danish sector of the North Sea (Upper Hauterivian to Albian), confirming the sequence of many of Jakubowski's events, and introducing several other potential datums (FOD of small *Rhagodiscus angustus* and FOD of *Flabellites oblongus*). This is the only North Sea biostratigraphical study to have been done entirely on the SEM, and thus has a degree of taxonomic surety not often seen in LM-based studies (but, conversely, a number of light-microscopically distinct species could not be separated on the SEM). Thomsen also pioneered a sample preparation technique that alleviated the problem of caving/downhole contamination, allowing FOs to be reliably recognised from ditch-cuttings. Recognising the relative lack of calibration of some Jakubowski's events against stage limits, Thomsen conducted a limited but thorough investigation of ammonite-dated Aptian outcrop material.

Crux (1989) re-investigated the Speeton section, and studied a number of German outcrop sections (notably Moorberg and Gott). He used his results to re-interpret Core 7B (previously dated by Aarhus *et al.*, 1986), from offshore mid-Norway. Crux produced a zonation scheme comprising 16 zones, spanning the Upper Ryazanian to Upper Barremian. The most notable new events recognised were the LO of *E.antiquus* (= *R.antiquus*), the LO of *"Stradnerlithus comptus"* (= *Clepsilithus maculosus*) and the LO of *Rhagodiscus pseudoangustus*. However, Crux, like previous authors, suffered from a lack of Upper Valanginian material, and could not place accurately a number of Late Valanginian-Early Hauterivian events. In addition, he was hampered by several broad species concepts (e.g. *"Tegumentum striatum"* = *Tegumentum bergeni* + *Eiffellithus* spp.). Crux was unable to successfully integrate his scheme with that of Jakubowski, due to the apparent rarity of several of Jakubowski's marker species (*C.cuvillieri*, *S.colligata*, *C.rothii*, and *N.borealis*), and different species concepts (*C.salebrosum*).

Fig. 3.1 - Compilation of Lower Cretaceous nannofossil datums recognised in the North Sea area. Taxonomy has been rationalised, as far as possible, to that used in the present study. Ages are those given by the various authors and are hence not always in agreement; the relative sequence of events in each study is more important.

Crux subsequently (1991) examined the Gault Clay (Middle and Upper Albian) of a Bedfordshire pit, finding the general sequence of nannofossil datums consistent with that reported from lower latitudes. He proposed a number of useful new datums - most notably the LOD of *Braloweria boletiformis* (= *Laguncula boletiformis*), the FOD of *Tegulalithus tessellatus* and the FOD of *Eiffellithus monechiae.* He disputed Jakubowski's use of the LO of common/abundant *Repagulum parvidentatum* as a Middle Albian datum, finding this species to be occasionally (but not consistently) common within the Upper Albian of this locality, and offshore mid-Norway.

Mutterlose (1991) documented the nannofloras of a large number of ammonite and belemnite-dated Valanginian-Aptian outcrops in N.W. Germany. Most significantly, he had access to thick, nannofossiliferous sections of Late Valanginian age, providing a more complete record of nannofloral development during this interval. He also documented more complete Late Barremian and Aptian onshore sections than had previously been examined in the Boreal area. Based solely on his own German material, Mutterlose proposed 13 zones spanning the Late Valanginian to Late Aptian, with a number of additional biohorizons based on *Nannoconus* acmes. He could not, however, integrate his zonation entirely successfully with the schemes of Jakubowski (1987) or Crux (1989), due to differing species concepts and incomplete stratigraphical coverage.

Bralower (1991) described the nannofossil biostratigraphy of Borehole 81/43 (re-examined in this study), which is closely comparable with the Speeton section on both lithological and micropalaeontological grounds (Lott *et al.*, 1986). He successfully applied Crux's (1989) zonation to the section, but paid particular attention to the distributions of several predominantly Tethyan nannofossil species (rare at Boreal latitudes). Based on the ranges of several such species (*T.verenae*, *C.cuvillieri*, and *S.colligata*), whose ranges had supposedly been well constrained in Tethyan sections, Bralower proposed that both the Valanginian-Hauterivian and Hauterivian-Barremian boundaries may have been considerably misplaced at Speeton. Perhaps most significantly, Bralower was able to place the LO of *T.striatum* (= *E.striatus*) within the range of *Tegulalithus septentrionalis*, in the Late Hauterivian (previous Boreal workers had much broader concepts of this species, giving it a much extended range). Bralower was, however, rather limited by his sample density, utilising only 50 "best-preserved" samples.

Having revised the taxonomy of the Polycyclolithaceae, Varol (1992) documented a number of important nannofossil datums (mainly LODs) in the Lower Cretaceous of the North Sea, finding most of these to be applicable world-wide. The most important datums documented include: LOD of *T.septentrionalis*, FOD of *F.varolii*, FOD of *R.planus* and *R.orbiculatus*, LOD of *F.varolii* and the LOD of *R.hollandicus*.

Jeremiah has recently (*in press*) proposed a very detailed nannofossil zonation for the Albian of the North Sea area, based on a thorough investigation of a number of onshore U.K. sections and North Sea wells. Twelve zones (labelled NAL 1-12, in ascending order) and a number of subzones are recognised, and the scheme offers resolution comparable with that attainable onshore by ammonites. The zones are defined using both FODs and LODs, but detailed abundance data enables identification of most zones from cutting material (using last common/abundant occurrences).

3.2.3 - Meanwhile elsewhere.....

The last ten years have seen significant advances in our understanding of the taxonomy and distribution of Lower Cretaceous nannofossils, due largely to a number of detailed DSDP and ODP studies. Wind & Cepek (1979), Roth (1983), Covington & Wise (1987), and Applegate & Bergen (1988) have given detailed descriptions of low-latitude Atlantic sections. Throughout these works there has been a steady refinement of taxonomic concepts, some of which Boreal workers have been slow to adopt (e.g. *Assipetra terebrodentarius*, *Eiffellithus windii*, *Eiffellithus striatus*), and a concomitant increase in biostratigraphical resolution.

Bralower *et al.* (1989) proposed a detailed subdivision of the Jurassic-Cretaceous boundary interval (Kimmeridgian to Lower Valanginian) of Tethys, based on a number of southern European and DSDP sections, and correlated their results with the geomagnetic polarity time scale. Unfortunately there is little hope of utilising this data in Boreal sections, since much of this interval is barren of nannofossils in the North Sea area.

Documentation of Lower Cretaceous nannofloras from high southern latitudes (Wise & Wind, 1977; Wise, 1983; Mutterlose & Wise, 1990; Mutterlose, 1992c; Bown, 1992) has shown similarities with Boreal assemblages, indicating that a number of species had bipolar distributions. The Neocomian sections of high southern latitudes have generally yielded more continuously ranging Tethyan marker species (e.g. *C.cuvillieri*) than encountered in the Boreal Realm; this perhaps reflects the better marine connections between these generally open, oceanic sites and tropical latitudes. Bown (1993) has utilised a mixed suite of "Boreal" and "Tethyan" marker species to date ODP sections in the Indian Ocean.

Most recently, Bergen (1994) has re-investigated the stratotypes of the Vocontian Trough, and DSDP Site 534 (western North Atlantic). Refined species concepts have enabled much improved resolution - a large number of events are correlatable between these two regions, on opposite sides of the Atlantic. Bergen disputes the ranges of

several species previously used in Tethyan zonations, and records a number of species previously thought to have been restricted to the Boreal area.

3.2.4 - The present 'state of the art' and reasons for revision

There has, until very recently, been a dichotomy among Lower Cretaceous nannopalaeontologists, with Boreal and Tethyan workers often unable to reconcile each others species concepts. Recent taxonomic refinements have shown that many species are common to both areas. Improved documentation of the ranges of such species has shown the potential for direct inter-regional correlation. Additionally, however, it has become apparent that the ranges of some species are strongly diachronous on an inter-regional (cross latitudinal) scale - such species are presumed to have had quite narrowly defined temperature tolerances, and the degree of diachroneity of their F/LODs must reflect changes in climatic regime or the degree of basin interconnectivity.

Even amongst Boreal nannopalaeontologists there have been differences in taxonomic concepts and, also, in the thoroughness of biostratigraphical logging. These problems have been compounded by the general incompleteness of onshore Lower Cretaceous sections. Thus, it has been impossible for any single author (other than, perhaps, Jakubowski, 1987) to examine a complete (even composite) nannofossiliferous section spanning more than a couple of stages. For these reasons, previous authors have found it difficult to fully integrate their respective zonation schemes.

Nevertheless, a large volume of published data now exists (much of it published during this study), and is available for comparison and re-interpretation. Thus, the range charts of previous authors were examined in detail, in order to fill in gaps in stratigraphical coverage and to confirm, or refute, the sequence of events observed in this study. The result is an attempt to reconcile the differences in previous zonations, and to calibrate the various events against one another.

3.3 - DISCUSSION OF THE SECTIONS

3.3.1 - Introduction

The bulk of the studied material is of Neocomian age - good overlap of sections throughout most of the Upper Ryazanian to mid-Barremian enables this interval to be confidently zoned and dated. Thus, the Neocomian sections are discussed first. The large number of samples from Speeton and Borehole 81/43 makes presentation of range charts impracticable in this section - these key sections are summarised by event diagrams (full range charts for all sections are given in the Appendix). Ammonite/belemnite-dated

outcrop sections are discussed first - the sequence of events established in these sections is subsequently used to date the offshore sections (wherever possible to an ammonite zone). Comments on individual sections are kept brief - it is hoped that the range charts and figures are largely self explanatory. All this information is subsequently used to compile a zonation scheme: the data presented in this section serves as a reference for the zones outlined in section 3.4.

The Aptian is an altogether more problematical stage, due to the often extreme condensation of this interval, and the unsuitability of its facies for nannofossil preservation; this interval is discussed separately and the, albeit fairly limited data from the studied sections is compiled with published data to reach some biostratigraphical conclusions.

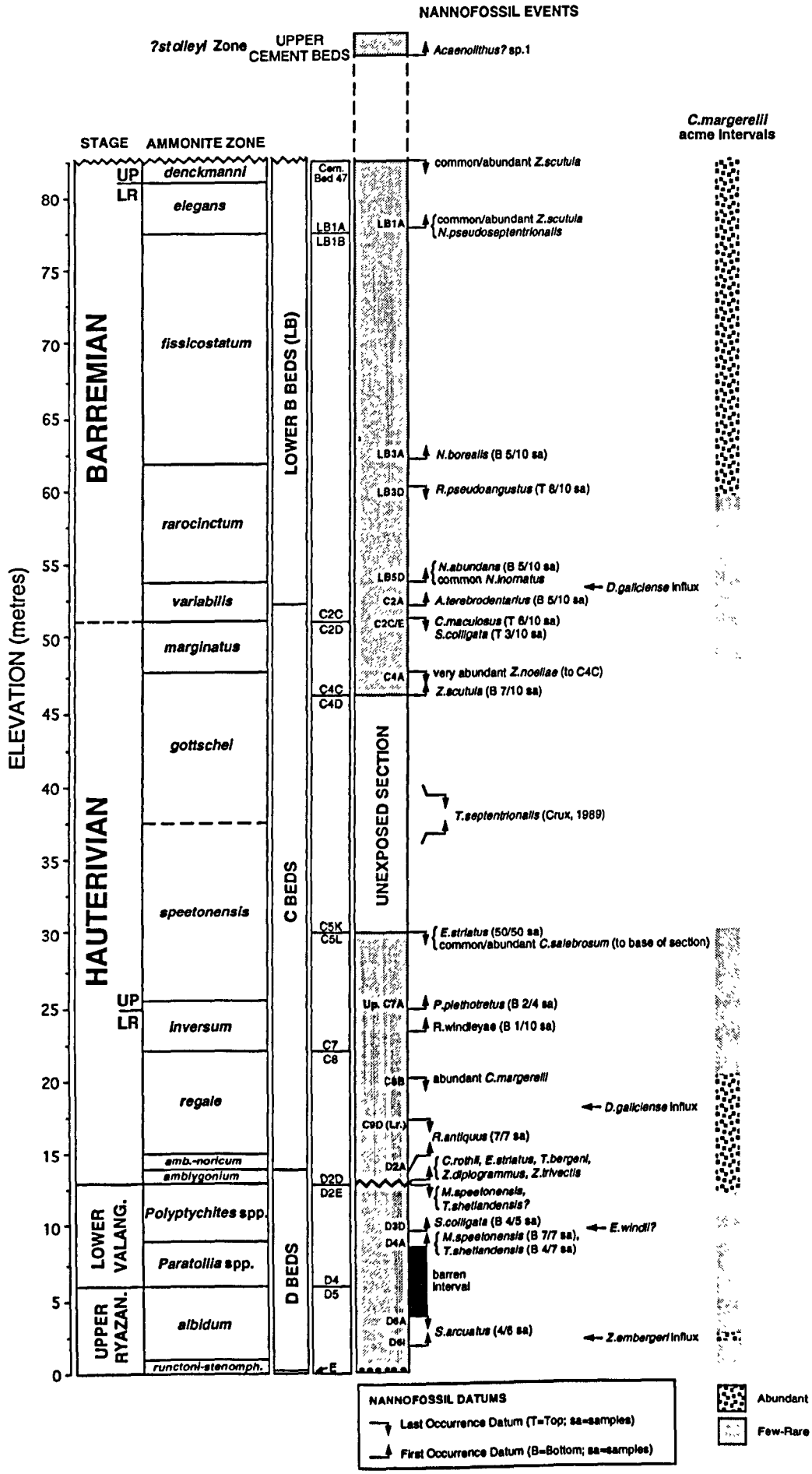
The only Albian material considered in this study is a very incomplete section from the upper part of the Heslerton Borehole; this section is zoned and dated using the recently proposed zonation of Jeremiah (*in press*), and the interval is not considered any further.

3.3.2 - Speeton

(see Fig.3.2 and Appendix Chart 1)

Nannofossil preservation - This is patchy in the Upper Ryazanian and Lower Valanginian, but consistently good throughout the Hauterivian and Barremian.

Upper Ryazanian-Lower Valanginian - Bed D7E yields the oldest well-preserved nannoflora; this moderately diverse assemblage contains *Cretarhabdus angustiforatus.* The remainder of the *albidum* Zone (Late Ryazanian) is characterised by *Nannoconus* sp. (disks), *Sollasites* spp. (with, generally rare, *Sollasites arcuatus*) and abundant *C.salebrosum.* A very marked influx of (abundant) *Zeugrhabdotus embergeri* occurs in Beds D6I-D6G. The uppermost *albidum* Zone and lower *Paratollia* spp. Zone are barren of nannofossils; *S.arcuatus* disappears across this barren interval, while *Micrantholithus speetonensis* and *Triquetrorhabdulus shetlandensis* appear immediately above. *Speetonia colligata* first appears *en mass* in the lower *Polyptychites* spp. Zone; this belated (relative to Tethys) FO is associated with a brief, but spectacular *Apertasphaera jakubowskii* acme (Beds D3C-D). The remainder of the Lower Valanginian is characterised by *M.speetonensis* and *T.shetlandensis*, with abundant *C.salebrosum.* A single, indeterminate specimen of *Eiffellithus* (*E.windii?*) was recorded in Bed D3C; this represents the oldest record of this important lineage.


NANNOFOSSIL EVENTS
?stradleyi Zone
UPPER CEMENT BEDS
Acaenolithus? sp.1
C.margerelii acme intervals
STAGE
AMMONITE ZONE
ELEVATION (metres)
BARREMIAN
HAUTERIVIAN
LOWER VALANG.
UPPER RYAZAN.
UP
LR
denckmanni
elegans
fissicostatum
rarocinctum
variabilis
marginatus
gottschei
speetonensis
inversum
regale
amb.-noricum
amblygonium
Polyptychites spp.
Paratollia spp.
albidum
runctoni-stenomph.
LOWER B BEDS (LB)
C BEDS
D BEDS
Cem. Bed 47
LB1A
LB1B
LB3A
LB3D
LB5D
C2A
C2C
C2C/E
C2D
C4A
C4C
C4D
C5K
C5L
Up. C7A
C7
C8
C8B
C9D (Lr.)
D2A
D2D
D2E
D3D
D4A
D4
D5
D6A
D6I
E
UNEXPOSED SECTION
common/abundant Z.scutula
common/abundant Z.scutula
N.pseudoseptentrionalis
N.borealis (B 5/10 sa)
R.pseudoangustus (T 6/10 sa)
N.abundans (B 5/10 sa)
common N.inornatus
D.galiciense influx
A.terebrodentarius (B 5/10 sa)
C.maculosus (T 6/10 sa)
S.colligata (T 3/10 sa)
very abundant Z.noeliae (to C4C)
Z.scutula (B 7/10 sa)
T.septentrionalis (Crux, 1989)
E.striatus (50/50 sa)
common/abundant C.salebrosum (to base of section)
P.plethotretus (B 2/4 sa)
R.windleyae (B 1/10 sa)
abundant C.margerelii
D.galiciense influx
R.antiquus (7/7 sa)
C.rothii, E.striatus, T.bergeni, Z.diplogrammus, Z.trivectis
M.speetonensis, T.shetlandensis?
S.colligata (B 4/5 sa)
E.windii?
M.speetonensis (B 7/7 sa), T.shetlandensis (B 4/7 sa)
barren interval
S.arcuatus (4/6 sa)
Z.emberger influx
0
5
10
15
20
25
30
35
40
45
50
55
60
65
70
75
80
NANNOFOSSIL DATUMS
Last Occurrence Datum (T=Top; sa=samples)
First Occurrence Datum (B=Bottom; sa=samples)
Abundant
Few-Rare

Hauterivian-Barremian - A major stratigraphical break between Beds D2E and D2D is manifest by a marked increase in nannofloral diversity, reflecting the origination of numerous species in the (missing) Upper Valanginian. *C.rothii*, *T.bergeni*, *E.striatus*, *Haqius* spp., *Z.diplogrammus* and *Z.trivectis* first appear immediately above this break, in the basal Hauterivian; *M.speetonensis* has its LO just below this boundary and *T.shetlandensis* has its last (possibly reworked) occurrence just above, in Bed D2D. *Radiolithus antiquus* first appears in Bed D2A; this distinctive species is restricted to a 4m thick, condensed sequence (Beds D2A-C9D(basal); 7/7 sa) spanning the upper *amblygonium* to lower *regale* Zones. *Cyclagelosphaera margerelii* is very abundant throughout this interval, but declines markedly in abundance in the upper *regale* Zone, a few metres above the LO of *R.antiquus*. The only significant event in the remainder of the continuously exposed lower-mid Hauterivian is the FO of *Perissocyclus plethotretus* (B 2/4 sa) in Bed C7A (uppermost *inversum* Zone). There follows a substantial sampling gap (Beds C5K-C4D; 15.5m); Crux (1989) recorded common *T.septentrionalis* in a single, unplaced sample from this interval. Several events are very noticeable across this gap - the LO of *E.striatus* (which is common throughout the underlying Hauterivian, occurring in 50/50 sa), the FO of *Zeugrhabdotus scutula*, and a dramatic reduction in the abundance of *C.salebrosum*. Assemblages from the exposed part of the *gottschei* Zone, immediately above this gap, are dominated by *Zeugrhabdotus noeliae*, which is much depleted in abundance in the overlying *marginatus* Zone. *S.colligata* has its LO (T 3/10 sa) in the *marginatus* Zone; the LO of *C.maculosus* is only centimetres above, in the basal *variabilis* Zone (T 10/15 sa). *T.bergeni* var. *minor* first appears in the lower *variabilis* Zone, and *Assipetra terebrodentarius* in the upper part of this zone. *Rhagodiscus pseudoangustus* and *Cretarhabdus inequalis* are relatively common in the *variabilis* Zone, and characteristic of this interval. The FO of *Nannoconus abundans* (B 5/10 sa) coincides with the base of the overlying *rarocinctum* Zone; this appearance is associated with a dramatic increase in the abundance of the closely-related *N.inornatus*. *A.terebrodentarius* is common throughout the *rarocinctum* Zone, while *C.margerelii* becomes abundant in the upper part; the LO of *R.pseudoangustus* (T 8/10 sa) was observed towards the top of this zone. The FO of *Nannoconus borealis* (B 5/10 sa) is approximately coincident with the base of the *fissicostatum* Zone; this zone is characterised by common/abundant *Nannoconus* spp. (*N.abundans* group), *Micrantholithus* spp. and *C.margerelii*, with very abundant *Rhagodiscus asper*. There is a very marked increase in the abundance of *Z.scutula* in the lower part of the *elegans* Zone; this large and conspicuous species remains consistently abundant throughout the remaining continuous exposure (into the *denckmanni* Zone). The *elegans* Zone is also characterised by common *Nannoconus pseudoseptentrionalis*. *Z.scutula* is markedly reduced in abundance in the Upper Cement Beds (*?stolleyi* Zone), in which the FO of *Acaenolithus?* sp.1 is observed.

Fig. 3.2 (facing) - Summary of nannofossil events observed in the Speton section.

3.3.3 - German outcrop material (composite section)

(see Appendix Chart 2)

Valanginian (Sachsenhagen & Hasselage) - A sparsely nannofossiliferous sample from the Early Valanginian *Platylenticeras robustum/heteropleuron* Zone of Sachsenhagen Pit is notable for yielding *T.shetlandensis*, without *M.speetonensis*, suggesting that the FO of the former species predates that of the latter. A single sample form the Late Valanginian *Dichotomites crassus* Zone of Hasselage yields a similarly dissolution-modified nannoflora, which nevertheless contains fairly common *E.windii* (*M.speetonensis* and *E.striatus* are notably absent).

Lower Hauterivian (Moorberg) - The Early Hauterivian nannofloras of Moorberg are well-preserved, diverse, and directly comparable with those of Speeton; the FO of *R.antiquus* lies within the *amblygonium* Zone, above the FOs of *C.rothii* and *E.striatus*, and this species occurs consistently (4/4 sa) throughout the upper *amblygonium* to *regale* Zones, in association with very abundant *C.margerelii*. *E.windii* is present in the *amblygonium* Zone, but always subordinate to *E.striatus*. As at Speeton, these nannofloras exhibit quite a strong Tethyan influence, with strictly warm-water species such as *Calcicalathina oblongata* making rare appearances. The only notable differences between this section and Speeton are the absence of *Calculites* spp., the presence of common/abundant *Stradnerlithus silvaradius* in the *amblygonium* Zone, and the slightly earlier FO of *Scapholithus fossilis* (in the *regale* Zone, within the range of *R.antiquus*).

Upper Hauterivian (Moorberg) - Five samples from the Late Hauterivian of Moorberg are equivalent to the unexposed C4-C5 interval (*speetonensis-gottschei* Zones) at Speeton, and enable some constraining of the events observed on either side of this sampling gap. *T.septentrionalis* is common/abundant in 4/4 of these samples, and disappears suddenly in the mid-*gottschei* Zone. *E.striatus* disappears suddenly in the upper *staffi* (= *speetonensis*) Zone, within the range of *T.septentrionalis*. *C.salebrosum* is rare throughout this sampled interval, indicating that this species suffered heavy depletion prior to the LO of *E.striatus*. The FO of *Z.scutula* was recorded in the *staffi* Zone. One sample, from the uppermost *staffi* Zone, yielded abundant *C.margerelii* (this brief acme is correlatable with Borehole 81/43). The highest sample from this section, from just above the LO of *T.septentrionalis*, yields very abundant *Z.noeliae*, signalling the start of a rather longer-term acme that seems to be regionally correlatable.

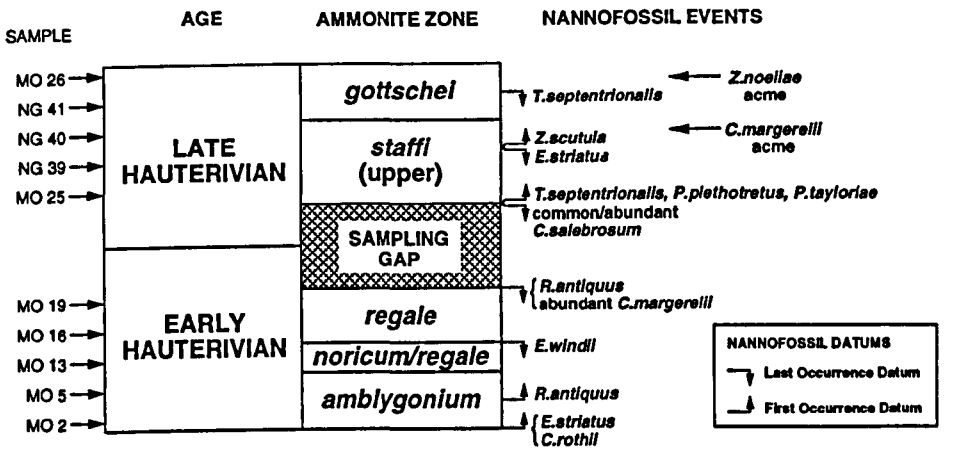


Fig. 3.3 - Summary of nannofossil events recognised in the Moorberg section.

Hauterivian/Barremian? (Frielingen) - The Hauterivian-Barremian boundary is generally placed at the top of the *discofalcatus* Zone in Germany, in a younger position to the *marginatus-variabilis* zonal boundary utilised at Speeton. Based on the absence of *C.maculosus*, *A.terebrodentarius*, and *N.abundans*, the two *discofalcatus* Zone samples from Frielingen are assignable to the *variabilis* Zone, and thus to the basal Barremian, if the stage-limits applied at Speeton are adopted (see further discussion under Zone BC 11).

Barremian (Gott) - Hauptblätterton assemblages are very similar to those from the *fissicostatum* Zone of Speeton, being of low diversity and dominated by *R.asper*, *C.margerelii*, *Micrantholithus* spp. and *Nannoconus* spp.. The only anomalous character is the absence of fully-developed *N.borealis* (although *N.borealis* var.A was recorded). The imprecisely-located samples from the *?germanica* Zone yield abundant *Z.scutula*, with *Acaenolithus?* sp.1 (= the *"V.matalosa"* of Crux, 1989, and Mutterlose, 1991), and are thus equivalent to part of the Cement Beds at Speeton. Two samples from the *depressa* Zone are entirely barren of nannofossils.

3.3.4 - Borehole 81/43

(see Fig. 3.4 and Appendix Chart 3)

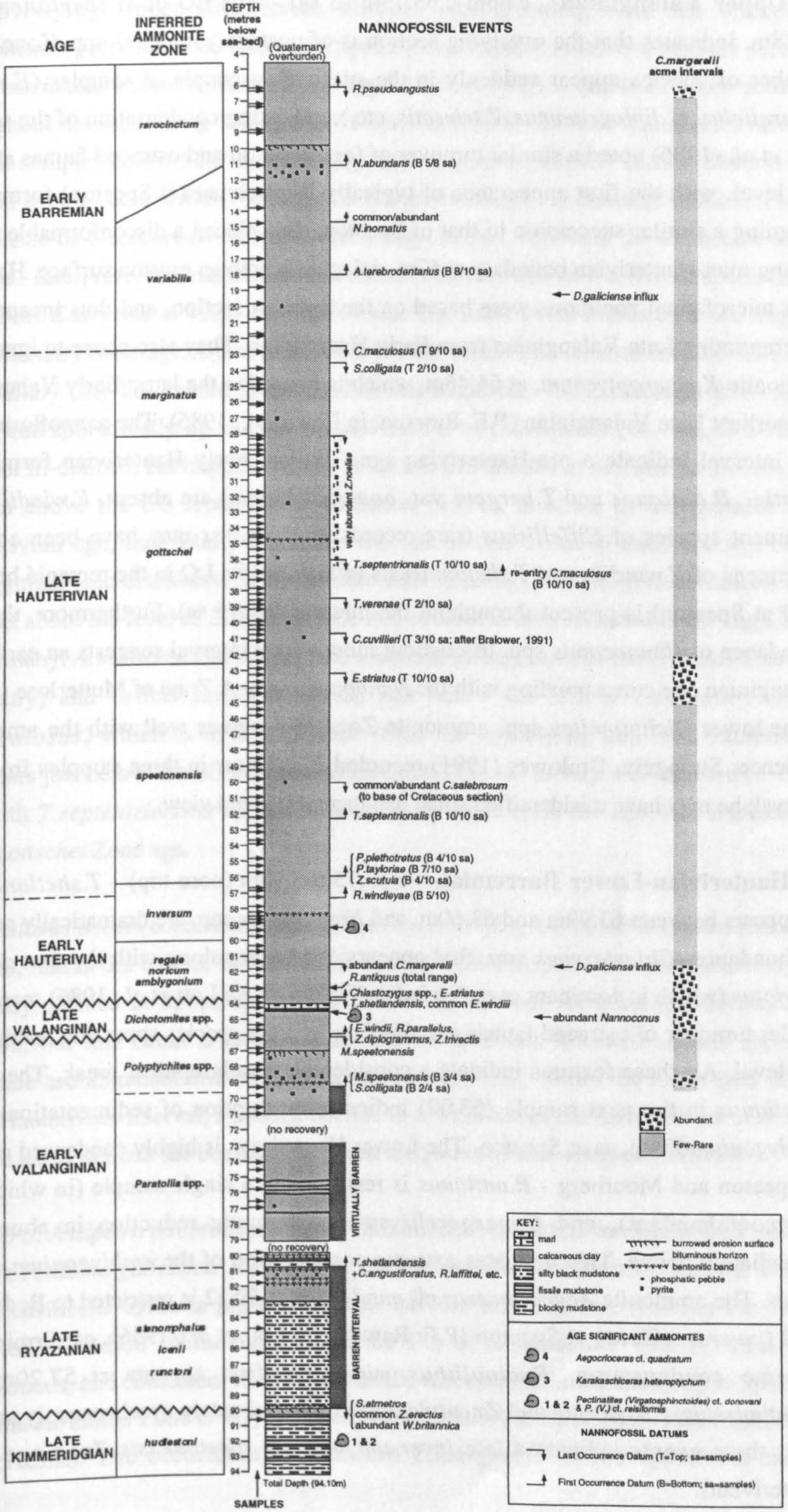
Nannofossil preservation - This is very patchy below 66m, with much of this interval entirely barren, but consistently good throughout the remainder of the core.

This section can be subdivided into 4 distinct units, separated by stratigraphical breaks:

(1) Upper Kimmeridgian - 94.10m (T.D.)-89.87m - This interval is dated by means of ammonites to the *hudlestoni* Zone, in the Upper Kimmeridgian (Lott *et al.*, 1986). Nannofossiliferous samples from 90.45m and 89.20m (the latter probably mis-measured) confirm this age assignment. These samples yield very abundant *Watznaueria britannica*, with common/abundant *Zeugrhabdotus erectus* and *Stephanolithion atmetros*, and lack most typical Cretaceous species (most notably *Z.embergeri*, *R.laffittei*, *Helenea* spp., and diverse cretarhabdaceans). Applying the nannofossil zonations of Bown & Cooper (1988) and Bralower *et al.* (1988) these samples are dated to the Upper Kimmeridgian (*sensu anglico*). If this entire interval belongs to the *hudlestoni* Zone (Lott *et al.* did not document the precise levels of the age diagnostic ammonites), then the presence of *S.atmetros* necessitates lowering of the lower boundary of the *S.atmetros* Zone of Bown *et al.*, 1988. This useful marker species seems to be restricted to the Boreal area.

(2) Upper Ryazanian-Lower Valanginian - 89.87m-c.66m - The interval below 80.31m is barren of nannofossils (and calcareous microfauna - Lott *et al.*, 1986), but has been lithostratigraphically correlated with the lower D-Beds (*stenomphalus-albidum* Zones) of Speeton by Lott *et al.* (1986), using a distinctive phosphatic nodule bed (= the Coprolite Bed) and a series of bentonites; this correlation has been supported by palynological data in Lott *et al.*, 1989. *T.shetlandensis*, at 80.31m, indicates a latest Ryazanian or Early Valanginian (*Paratollia* spp. Zone) age. This suggests that the highest of the group of four bentonites (bentonite (4)) which Lott *et al.* (1986, 1989) correlated with Speeton is rather younger than these authors believed, and not equivalent to a bentonite in the upper part of Bed D6; bearing in mind the varying degrees of condensation in these two sections, and the incompleteness of core recovery in this part of Borehole 81/43, it seems unlikely that 4 thin bentonites would have matched exactly. The overlying interval is only sparsely nannofossiliferous; *M.speetonensis* appears at 69.32m, confirming a FO above that of *T.shetlandensis*, and an Early Valanginian (*Paratollia* or *Polyptychites* spp. Zone) age.

Fig. 3.4 (facing) - Summary of nannofossil events observed in Borehole 81/43.


AGE
INFERRED AMMONITE ZONE
DEPTH (metres below sea-bed)
NANNOFOSSIL EVENTS
(Quaternary overburden)
C.margerelii acme intervals
EARLY BARREMIAN
rarocinctum
variabilis
LATE HAUTERIVIAN
marginatus
gottschei
EARLY HAUTERIVIAN
speetonensis
inversum
regale
noricum
amblygonium
LATE VALANGINIAN
Dichotomites spp.
Polyptychites spp.
EARLY VALANGINIAN
Paratollia spp.
LATE RYAZANIAN
albidum
stenomphalus
icenii
runctoni
LATE KIMMERIDGIAN
hudlestoni
R.pseudoangustus
N.abundans (B 5/8 sa)
common/abundant N.inornatus
A.terebrodentarius (B 8/10 sa)
D.galiciense influx
C.maculosus (T 9/10 sa)
S.colligata (T 2/10 sa)
very abundant Z.noelae
T.septentrionalis (T 10/10 sa)
re-entry C.maculosus (B 10/10 sa)
T.verenae (T 2/10 sa)
C.cuvillieri (T 3/10 sa; after Bralower, 1991)
E.striatus (T 10/10 sa)
common/abundant C.salebrosum (to base of Cretaceous section)
T.septentrionalis (B 10/10 sa)
P.plethotretus (B 4/10 sa)
P.tayloriae (B 7/10 sa)
Z.scutula (B 4/10 sa)
R.windleyae (B 5/10)
4
abundant C.margerelii
R.antiquus (total range)
D.galiciense influx
Chiastozygus spp., E.striatus
T.shetlandensis, common E.windii
3
abundant Nannoconus
E.windii, R.parallelus, Z.diplogrammus, Z.trivectis
M.speetonensis
M.speetonensis (B 3/4 sa)
S.colligata (B 2/4 sa)
(no recovery)
VIRTUALLY BARREN
(no recovery)
T.shetlandensis +C.angustiforatus, R.laffittei, etc.
BARREN INTERVAL
S.atmetros
common Z.erectus
abundant W.britannica
1 & 2
Total Depth (94.10m)
SAMPLES
Abundant
Few-Rare
KEY:
marl
calcareous clay
silty black mudstone
fissile mudstone
blocky mudstone
burrowed erosion surface
bituminous horizon
bentonitic band
phosphatic pebble
pyrite
AGE SIGNIFICANT AMMONITES
4 Aegocrioceras cf. quadratum
3 Karakaschiceras heteroptychum
1 & 2 Pectinatites (Virgatosphinctoides) cf. donovani & P. (V.) cf. reisiformis
NANNOFOSSIL DATUMS
Last Occurrence Datum (T=Top; sa=samples)
First Occurrence Datum (B=Bottom; sa=samples)

(3) Upper Valanginian - c.66m-c.63.75m (5 sa) - The LO of *M.speetonensis*, at 66.28m, indicates that the overlying section is of post-*Polyptychites* spp. Zone age; a number of species appear suddenly in the succeeding couple of samples (*E.windii*, *R.parallelus*, *Z.diplogrammus*, *Z.trivectis*, etc.), indicating condensation of the section. Lott *et al.* (1986) noted a similar turnover of foraminiferal and ostracod faunas at about this level, with the first appearance of typically Hauterivian (at Speeton) forms, and, assuming a similar succession to that of Speeton, they placed a disconformable Lower Valanginian-Hauterivian boundary at 67m, coinciding with an erosion surface. However their microfaunal zonations were based on the Speeton section, and thus incapable of differentiating Late Valanginian from Early Hauterivian. They also chose to ignore the ammonite *K.heteroptychum*, at 64.46m, which is limited to the latest Early Valanginian and earliest Late Valanginian (P.F. Rawson, in Lott *et al.*, 1986). The nannofloras from this interval indicate a pre-Hauterivian age - typical Early Hauterivian forms (e.g. *C.rothii*, *R.antiquus* and *T.bergeni* var. *quasioctiformis*) are absent, *E.windii* is the dominant species of *Eiffellithus* (rare records of *E.striatus* may have been aberrant specimens of *E.windii*), and *T.shetlandensis* (which has its LO in the remanié horizon, D2D at Speeton) is present throughout the interval (in 4/5 sa). Furthermore, the high abundance of *Nannoconus* spp. throughout most of this interval suggests an early Late Valanginian age corresponding with the *Nannoconus* spp.A Zone of Mutterlose (1991), in the lower *Dichotomites* spp. ammonite Zone; this agrees well with the ammonite evidence. Strangely, Bralower (1991) recorded *R.antiquus* in three samples from this interval; he may have misidentified small nannoconids in end view.

(4) Hauterivian-Lower Barremian - c.63.75m-6.12m (core top) - *T.shetlandensis* disappears between 63.99m and 63.60m, and *Nannoconus* spp. are dramatically reduced in abundance. *Chiastozygus* spp. first appears at 63.60m, along with the first definite *E.striatus* (which is dominant over *E.windii*). Wilkinson (*in* Lott *et al.*, 1986) recorded a similar turnover of ostracod faunas at c.63.60m, with six species appearing suddenly at this level. All these features indicate a considerable stratigraphical break. The FO of *R.antiquus* in the next sample (63.02) indicates resumption of sedimentation in the *amblygonium* Zone, as at Speeton. The Lower Hauterivian is highly condensed relative to Speeton and Moorberg - *R.antiquus* is restricted to a single sample (in which it is common/abundant), and *C.margerelii* suffers dramatic reduction in abundance immediately above. This indicates extreme condensation of the *amblygonium-regale* Zones. The ammonite *Aegocrioceras* cf. *quadratum* at 59.12 is restricted to Beds C7F-C7G (*inversum* Zone) at Speeton (P.F. Rawson, in Lott *et al.*, 1986), confirming this extreme condensation. *Rucinolithus windleyae* first appears at 57.20m, and *P.plethotretus*, *P.tayloriae* and *Z.scutula* appear approximately synchronously at about 56m; these events indicate a late *inversum* or early *speetonensis* Zone age (mid-Hauterivian).

The overlying Upper Hauterivian section, corresponding with the unexposed *speetonensis-gottschei* Zone interval at Speeton, is expanded relative to onshore sections. *T.septentrionalis* makes a dramatic first appearance at 52.23m, and is common/abundant throughout the succeeding 16m (36 sa); Bralower (1991) recorded this species rarely in several samples below 52.23m, so it may have originated slightly earlier. Several very marked events occur within the range of *T.septentrionalis* - a dramatic reduction in the abundance of *C.salebrosum* at c.50m (this may, in fact, represent the extinction of this species - later, rare, records may be reworked or attributable to a different species), and the LO of *E.striatus* at 43.24m (T 10/10 sa). The latter event indicates a late *staffi* (= *speetonensis*) Zone age. Other less useful events within this interval include the LO of *C.cuvillieri* (my last record is at 51.37m, but Bralower, 1991, recorded this species rarely and sporadically up to 40.78m) and the FO of *C.inequalis* (44.46m, B 1/10 sa). Another ill-defined, but important event is the LO of *Tubodiscus verenae*, at 38.66m; this is 15m above the LO recorded by Bralower (1991), in strata of indisputable Late Hauterivian age, and totally discredits the use of this event to mark the top of the Valanginian (see discussion in Systematic Palaeontology). *C.margerelii* forms a brief acme at about the level of *E.striatus'* LO; this event was also recorded in the *staffi* Zone of Germany. *A.infracretacea* is common/abundant throughout this interval (more so than Germany) and suffers heavy depletion just below the LO of *T.septentrionalis*. *C.maculosus*, which is notably absent from the underlying mid-late Hauterivian, reappears just below the LO of *T.septentrionalis*. This LO is very well-defined (T 10/10 sa), with *T.septentrionalis* occurring abundantly right up to the end, and indicates an early *gottschei* Zone age.

C.maculosus occurs consistently throughout the overlying 14m (26/28 sa) and its LO, at 22.90m, marks the base of the *variabilis* Zone (= Hauterivian-Barremian boundary, as currently defined at Speeton); the LO of *S.colligata* was recorded just below, as at Speeton, but this event is less well-defined (T 2/10 sa). *Micrantholithus* spp. and *Z.noeliae* are abundant and very abundant, respectively, within the lower part of this latest Hauterivian interval; a sudden decline in abundance of the latter species at 28.10m may be taken to mark the boundary between the *gottschei* and *marginatus* Zones.

The FO of *Assipetra terebrodentarius*, at 18.00m, indicates a mid-*variabilis* Zone age. An influx of *Diloma galiciense* at about this level is also correlatable with Speeton. The top of the *variabilis* Zone is placed between 14.70m and 11.01m, between the FO of common/abundant *N.inornatus* and the FO of *N.abundans* (these events are synchronous, and coincident with the *variabilis-rarocinctum* zonal boundary at Speeton). Thus the *variabilis* Zone is very much expanded relative to Speeton (6-10m thick, rather than c.2.5m). The occurrence of abundant *C.margerelii* in the uppermost sample

(6.12m), and the continued presence of *R.pseudoangustus* are indicative of a mid-upper *rarocinctum* Zone age (Early Barremian).

3.3.5 - Core 7B (offshore mid-Norway)

(see Fig. 3.5 and Appendix Chart 4)

Nannofossil preservation - The shales below 11.00m are barren of nannofossils, with the exception of a few dissolution-resistant *Watznaueria* at 12.00m. The remainder of the section is nannofossiliferous - the limestone horizon (11.00-8.00m) yields moderately overgrown assemblages, while the overlying marls yield better-preserved nannofloras.

C.salebrosum is so abundant in the interval 10.75-8.00m that the standard counting procedure was modified, to count at least 500 nannofossils per slide, in order to obtain more representative species abundance ratios. This modified counting procedure was maintained for the remainder of the core. The nannofossiliferous part of this section can be subdivided into two intervals, separated by a major stratigraphical break:

(1) Upper Ryazanian-basal Valanginian - 11.00-8.00m - *S.arcuatus*, at 10.95-10.77m, is indicative of a latest Ryazanian (*albidum* Zone) age. Other characteristic elements of this interval include *Sollasites lowei, Kokia borealis*, common/abundant *C.salebrosum*, and common *C.margerelii.* The LO of *Sollasites arcuatus* at 10.77m is a close approximation of the Ryazanian-Valanginian boundary. *Kokia curvata, Kokia borealis* and *Nannoconus oviformis* are common in the overlying 1.5m; the latter two species apparently dying out before the FO of *T.shetlandensis*, at 8.20m. The presence of *T.shetlandensis* and *Micrantholithus brevis*, without *Micrantholithus speetonensis*, is indicative of a earliest Valanginian (lower *Paratollia* spp. Zone) age. *Perissocyclus fletcheri* (at 9.80m) has only previously been recorded from the Late Ryazanian.

(2) Upper Hauterivian - 7.35-4.50m - A massive nannofloral turnover between 8.00m and 7.35m (unrecovered section) reflects a major break in the succession. *C.salebrosum*, which dominates nannofloras below 8.00m, is rare or absent above this level, while *T.shetlandensis,* and *Kokia* spp. disappear at this major disconformity. *Chiastozygus* spp., *Conusphaera rothii, Tegumentum bergeni, Tegumentum octiformis, Lithraphidites bollii, Perissocyclus plethotretus, Tranolithus gabalus, Zeugrhabdotus diplogrammus, Zeugrhabdotus scutula* and *Zeugrhabdotus trivectis* first appear immediately above. Most of these species originate in the Valanginian, but *P.plethotretus* and *Z.scutula* are first recorded in the mid-Hauterivian. The complete omission of both *Eiffellithus striatus* (Late Valanginian-Late Hauterivian) and *Tegulalithus septentrionalis*

(Late Hauterivian) from this section, coupled with the massive depletion of *C.salebrosum*, indicates that sedimentation resumed no earlier than the *gottschei* Zone (Late Hauterivian). The presence of *Clepsilithus maculosus* up to 4.80m (Crux, 1989, recorded this species up to 4.50m) indicates an age no younger than basal *variabilis* Zone. *Z.noeliae* is extremely abundant between 7.35 and 5.10m, and suffers sudden and heavy depletion above this; this acme was observed within the Late Hauterivian part of *C.maculosus'* range at both Speeton and Borehole 81/43, and its top is an accurate approximation for the *gottschei-marginatus* ammonite zonal boundary.

Crux (1989) recorded *M.speetonensis* and *T.septentrionalis* at 7.35m; neither species was recorded in the present study but, if present, they were almost certainly reworked from the missing section. Crux's concept of "*Tegumentum striatum*" was much wider than that applied here to *Eiffellithus striatus* - the "*T.striatum*" he logged above 7.35m is a small, long-ranging form assigned herein to *Tegumentum bergeni*.

3.3.6 - Core 7425/9-U-1 (Barents Sea)

(see Fig. 3.5 and Appendix Chart 5)

Nannofossil Preservation - This is poor to moderate throughout the entire core. The carbonate-rich units yield overgrown nannofloras, while assemblages from the siltstones are strongly etched. Nevertheless, few samples were entirely barren and most yielded age diagnostic assemblages.

This core can be subdivided into three units, separated by stratigraphical breaks:

(1) Upper Ryazanian-Lower Valanginian - 65.60m (TD)-c.57m - The presence of *S.arcuatus* up to 64.28m is indicative of a latest Ryazanian age. This agrees with the macrofossil and foraminifera-based date of Århus, 1991. Other characteristic elements of this interval include *K.borealis*, common/abundant *C.salebrosum* and common *Sollasites* spp. (especially *S.lowei*). *C.angustiforatus*, which occurs in the basal sample (65.60m), first appears in the Berriasian (Bralower *et al.*, 1988) of Tethyan regions. The disappearance of *S.arcuatus* and reduction in abundance of *Sollasites* spp. at 64.00m may be taken to mark the Ryazanian-Valanginian boundary. Characteristic Valanginian elements in the overlying interval include *K.curvata, T.shetlandensis* and common/abundant *C.salebrosum*. As in Core 7B, *T.shetlandensis* first appears several metres above the LO of *S.arcuatus*. The absence of *Micrantholithus speetonensis*, which appears in the upper part of the *Paratollia* spp. Zone at Speeton, suggests that the whole of this interval falls within the lower part of this Zone. It is possible that *Micrantholithus speetonensis* may have been precluded from higher latitudes by environmental limitations

but, whatever the case, this interval is certainly Early Valanginian in age, due to the absence of *Eiffellithus* spp..

(2) Hauterivian - c.57m-c.55m - A large part of the Hauterivian is represented in highly condensed form, by two metres of nodular limestone. The LO of *T.shetlandensis* at 57.22, and the FOs of *E.striatus* and *R.antiquus* in the succeeding sample (56.92m) indicate a stratigraphical break, with resumption of sedimentation in the Early Hauterivian (*amblygonium-regale* Zone). The presence of common *C.margerelii* at 56.92m supports this age assignment; *R.antiquus* and common *C.margerelii* are restricted to this single sample, indicating extreme condensation of the Early Hauterivian. The LOs of *E.striatus* and common/abundant *C.salebrosum* at 55.50m, and the FO of *T.septentrionalis* in the same sample, indicate a *speetonensis* Zone age. The continued presence of *T.septentrionalis* at 55.20m suggests an early *gottschei* Zone age; its LO at this level corresponds with the top of the nodular limestone horizon.

(3) Basal Barremian - c.55m-49.72m (core top) - *C.maculosus*, which is characteristic of the latest Hauterivian (above the LO of *T.septentrionalis*) in North Sea sections, has not been proven to have ranged into the Barents Sea, so latest Hauterivian and earliest Barremian assemblages cannot yet be reliably differentiated. However, the presence of very small forms of *Tegumentum* (= *T.bergeni* var. *minor*) from 54.50m upwards suggests an Early Barremian age - this form is restricted to the *variabilis-rarocinctum* Zones at Speeton. The presence of common *R.pseudoangustus* from 52.50-51.00m, and the absence of *N.abundans*, limits the age of this interval to the *variabilis* Zone. The low abundance of *C.margerelii* throughout this interval supports this age assignation - this species becomes common in the *rarocinctum-fissicostatum* Zones at Speeton, but is quite rare in the *variabilis* Zone. An Early Barremian age for the marls and siltstones above 55.00m agrees with the interpretation of Århus (1991), based on palynological data.

3.3.7 - Core 7430/10-U-1 (Barents Sea)

(see Fig. 3.5 and Appendix Chart 6)

Nannofossil Preservation - The shales below 43.00m are essentially barren of nannofossils; a few samples yield dissolution-resistant *Watznaueria* (the relatively high proportion of *Watznaueria britannica* at 57.63m is suggestive of a Late Jurassic or earliest Cretaceous age). The overlying limestones and marls yield overgrown assemblages. The siltstones above 33.00m are only sparsely nannofossiliferous - occasional samples yield dissolution-modified assemblages.

The nannofossiliferous part of the core can be subdivided into three main units, separated by stratigraphical breaks:

(1) ?Uppermost Ryazanian-Lower Valanginian - 41.50m-c.38.75m - The possible presence of *S.arcuatus* (poorly preserved) at 41.50m suggests a latest Ryazanian age. This date coincides with the initiation of carbonate deposition elsewhere in the North Sea and Barents Sea. The overlying interval is dominated by *C.salebrosum*; the FO of *T.shetlandensis* at 39.57m indicates an Early Valanginian (*Paratollia* spp. Zone) age. The FO of fairly common *Tranolithus gabalus* coincides with the FO of *T.shetlandensis* - this event is also recognised in Core 7425/9-U-1, and in the Speeton section.

(2) 'Mid'-Hauterivian - c.38.75m-36.00m - *T.shetlandensis* disappears above 39.00m, and *E.striatus* first appears at 38.04m - these events indicate a Late Valanginian or younger age, but the absence of *R.antiquus* and the rarity of *C.margerelii* point to a late Early Hauterivian age. The FO of *P.plethotretus*, at 36.10m indicates a mid-Hauterivian (*inversum-speetonensis* Zone) age. The presence of *E.striatus* and abundant *C.salebrosum* up to 36.10m, and the absence of *Tegulalithus septentrionalis* at this level, indicate an age no younger than mid-*speetonensis* Zone. This interval encompasses the nodular limestone unit, which corresponds with a similar horizon in Core 7425/9-U-1; these nodular beds may be almost exactly equivalent in age - they are so condensed that species such as *R.antiquus* and *T.septentrionalis* may be restricted to inter-sample intervals. Århus (1991) dated this nodular limestone as Early Barremian, but this date was based on a single well-preserved dinoflagellate cyst in an otherwise barren sample from 38.00m, and on the rare occurrence of a foraminifer at 37.75m (unpublished data) - both specimens may have been contaminants.

(3) Barremian - c.36.00m?-11.20m (core top) - An abrupt lithological change at 36.00m (from nodular limestone to marl) is reflected by a dramatic turnover in the nannoflora. *C.salebrosum*, which dominates assemblages below 36.00m, disappears at this boundary, as does *E.striatus*. There are few age diagnostic nannofossils in the overlying marls, but the abrupt extinction of *C.salebrosum* and the absence of *T.septentrionalis* suggest a considerable break at 36.00m; it seems likely that sedimentation did not resume until the Early Barremian, which would fit with Århus' (1991) date for this interval (based on microfaunal and palynological data). *Conusphaera rothii*, at 34.12m, indicates that the marls are no younger than mid-Barremian. *P.plethotretus* is conspicuous throughout this interval, as it is in the Early Barremian of Speeton. The absence of *Nannoconus abundans* from the marl horizon suggests that it may be earliest Barremian (*variabilis* Zone) in age.

C.salebrosum, *E.striatus*, and *T.shetlandensis* are reworked at 32.67 - this assemblage indicates reworking down to the Valanginian. The overlying silts are very poorly nannofossiliferous. The first age-significant nannofossil, *Nannoconus pseudoseptentrionalis*, occurs at 24.30m and indicates a mid-Barremian age (this species appears at the base of the *elegans* Zone at Speeton). Sporadic occurrences of *Nannoconus abundans* in the silts above confirm a Barremian age. Large forms of *Cyclagelosphaera papilla* are conspicuous in the less-heavily etched samples above 22.90m; such forms are only conspicuous at Speeton in the mid-Barremian.

3.3.8 - Correlation of the Neocomian sections and implications for regional sequence stratigraphy

Boreal Lower Cretaceous sections tend to be very incomplete, with the degree of incompleteness increasing towards basin margins and structural highs, where unconformities combine to form major hiatuses (Rawson & Riley, 1982). Correlation of the studied sections (Fig. 3.5) demonstrates several regionally correlatable breaks. The most easily identified component of such breaks is the *transgressive surface*, formed by resumption of sedimentation after a period of non-deposition or erosion, and indicating the onset of sea-level rise. A number of such transgressive surfaces are readily identifiable (Fig. 3.6), and agree well with the sequence of events observed onshore (Rawson & Riley, 1982; Rawson, 1993; Rawson, *in press*) and corroborated rather less precisely in the North Sea by Rawson & Riley, 1982. These sea-level events are discussed below.

Late Ryazanian transgression. This flushed out the North Sea basin during the *stenomphalus* Zone, causing a major facies change from organic-rich shale (Kimmeridge Clay Formation) to calcareous mudrock (Valhall and Speeton Clay formations). This generally coincides with the sudden appearance of typically Cretaceous nannofloras - the underlying Kimmeridge Clay is barren or only very sparsely nannofossiliferous. Rawson and Riley (1982) demonstrated that "over most of the North Sea the base of the Valhall Formation is isochronous, and conformable with underlying sediments." Nevertheless there is often a considerable break at marginal sites (e.g. Speeton). This transgression affected the offshore Norwegian sections during the *albidum* Zone. Carbonate deposition did not, apparently, begin until rather later (late *albidum* or early *Paratollia* spp. Zone) in Borehole 81/43, although this may reflect another, basal Valanginian sea-level event (Rawson, *in press*).

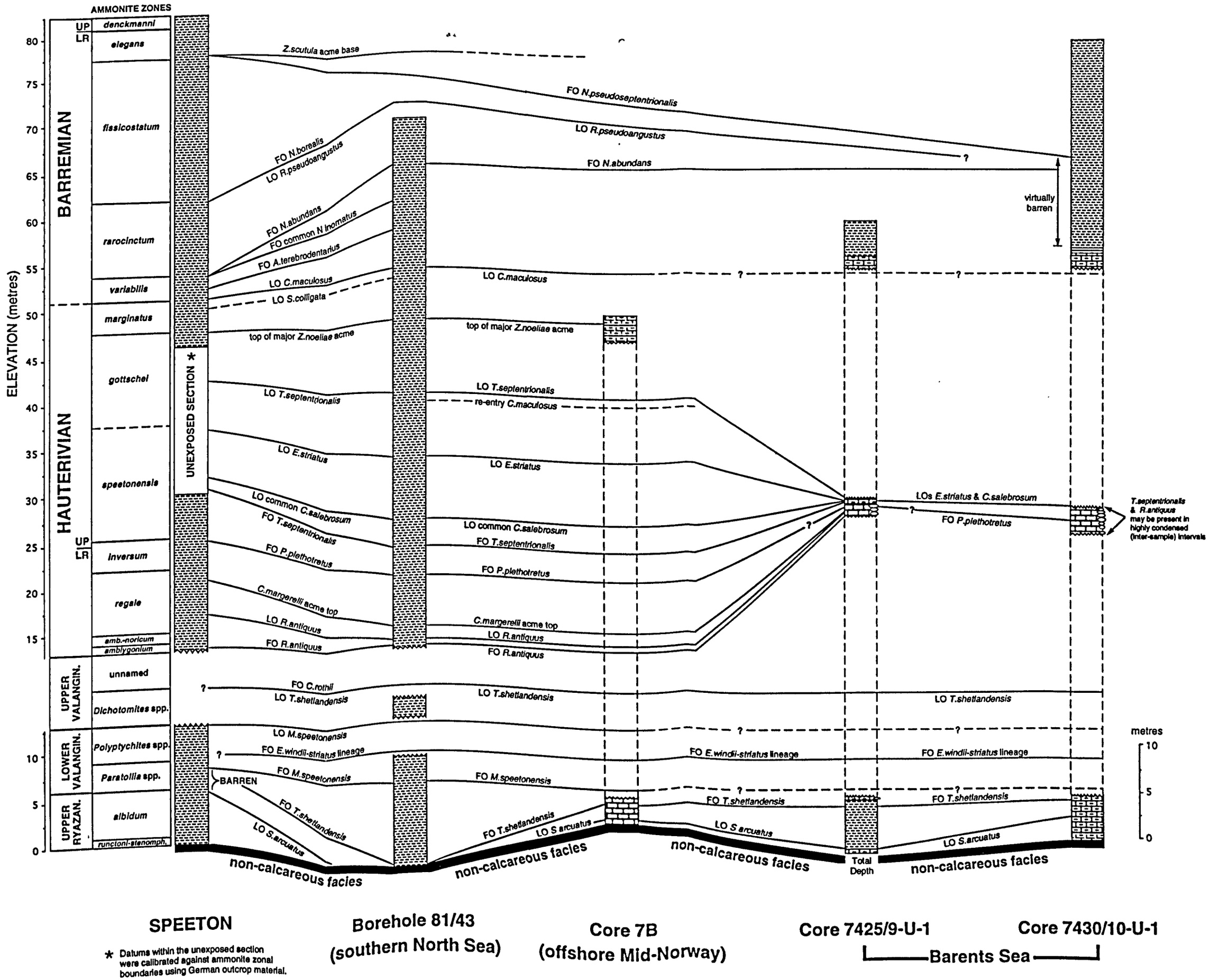


Fig. 3.5 - Correlation of the Neocomian sections. FO = first occurrence; LO = last occurrence.

PAGE

NUMBERING

AS ORIGINAL

'Mid'-Valanginian transgression. This affected much of Europe, and is especially clear in northern Germany (Rawson, *in press*). It is represented in Borehole 81/43, where a short section of early Late Valanginian strata (with *Karakaschiceras*) overlies a minor unconformity.

Earliest Hauterivian transgression. This is most pronounced at Speeton, where sedimentation resumed after a long break, but is also clearly identifiable in Borehole 81/43, and Core 7425/9-U-1.

'Mid'-Hauterivian transgressions. Rawson (*in press*) recognises two closely-spaced transgressive pulses in the mid-Hauterivian. The first of these, at the base of the *inversum* Zone, is marked by a major faunal turnover at Speeton. This event may be identifiable in Core 7430/10-U-1, where sedimentation seems to have resumed, after a long break, during the *inversum* Zone; however the section is so condensed that the Lower Hauterivian may be preserved between sample intervals (in <50cm). A second transgressive pulse, high in the *inversum* Zone, might be represented in Borehole 81/43 by the approximately synchronous FOs of four species (*R.windleyae*, *P.plethotretus*, *P.tayloriae* and *Z.scutula*), which suggests a stratigraphical break.

Late Hauterivian - Early Barremian transgressions. There is little onshore evidence of sea-level events during this interval - Rawson (*in press*) suggests that "sea-levels probably fluctuated but remained fairly high through the remainder of the Hauterivian and into the earliest Barremian." However, in Core 7B sedimentation resumed after a very long break during the late *gottschei* Zone; this might, of course, be the result of tectonic subsidence rather than sea-level rise, but it does agree well with the positioning of a Late Hauterivian sequence boundary by Haq *et al.*, 1988 (illustrated in Rawson, 1993 and Rawson, *in press*). Similarly, the two Barents Sea cores seem to have been affected by a *variabilis* Zone transgression, although this event is less confidently dated, since the latest Hauterivian markers utilised in more southerly sections are not yet proven to have ranged into the Barents Sea. A regional break at this level might explain the apparent absence of the latest Hauterivian marker species *C.maculosus* in Germany.

Fig. 3.6 - A comparison of the Neocomian sea-level events recognised in onshore N.W. Europe (Rawson, 1993; Rawson, *in press*) and transgressive surfaces recognised in this study (these are dated to ammonite zones using nannofossils).

3.3.9 - Ammonite-dated Aptian material

Onshore Aptian sections tend to be highly condensed, and/or in facies that are unlikely to yield nannofossils. Thus, I have compiled the data from my limited amount of definitely-dated, nannofossiliferous material with similarly limited data from Thomsen (1987) and Mutterlose (1991), in order to enable dating of the Aptian part of the Heslerton Borehole. I have also utilised the sequence of LOs recognised offshore by Jakubowski, 1987. This compilation is illustrated in Fig.3.7; the ammonite-dated material is discussed below.

Fig. 3.7 - Compilation of nannofossil range data for the Aptian of the North sea area, using ammonite-dated outcrop material (Thomsen, 1987; Mutterlose, 1991; this study) and the sequence of first downhole occurrences observed offshore (Jakubowski, 1987). Jakubowski's NLK zones are recalibated against the ammonite zones.

Skegness Clay (lower *fissicostatus* Zone (*bodei* Subzone)) (see Appendix Chart 8) - This represents the most basal Aptian deposit available. The most noteworthy feature of the five nannofossiliferous samples is the presence of small forms of *R.angustus* (subsp. *parvus*), indicating that this species evolved in the earliest Aptian. *Watznaueria britannica* is notably rare or absent. The uppermost sample assigned to this unit contains species known to have originated later in the Aptian (e.g. *Radiolithus orbiculatus*), and must have been miscollected.

Atherfield Clay (upper *fissicostatus* Zone (*obsoletus* Subzone)-lower *forbesi* Zone) (see Appendix Chart 7) - Most of the 75 samples examined are entirely barren of nannofossils; the only reasonable assemblages recovered are from the Perna Beds (3 samples) and the lower part of the Chale Clay (3 samples). A remarkable feature of the Perna Bed assemblages (*obsoletus* Subzone) is the high abundance (up to 15%) of *Watznaueria britannica*; this is a predominantly Jurassic species, which is very rare throughout the Neocomian. *W.britannica* is markedly reduced in abundance in the overlying Chale Clay. This brief influx event seems to be correlatable basin-wide - it is identified in the Heslerton Borehole, Germany (from a range chart of Mutterlose, 1991a, p.72), and the Danish Sector of the North Sea (from the range charts of Thomsen, 1987). *R.angustus parvus* and *C.margerelii* are abundant/very abundant in the few nannofossiliferous samples from the Chale Clay. *Farhania varolii, Flabellites oblongus* and *Hayesites irregularis* are notably absent from the Chale Clay samples (= lower *forbesi* Zone); Thomsen (1987) and Mutterlose (1991) recorded these species in the "Fischschiefer" (= upper *forbesi* Zone), indicating FOs within the *forbesi* Zone.

Gott marls (*nutfieldiensis* Zone) (see Appendix Chart 2) - These Upper Aptian marls lie unconformably upon Upper Barremian clays and, as might be expected in such a transgressive deposit, they show considerable evidence of reworking - *E.striatus*, *T.septentrionalis* and *C.salebrosum* indicate reworking down to the Upper Hauterivian. *Crucibiscutum* is particularly abundant, but most specimens seem subtly different to Neocomian specimens of *C.salebrosum*, and are thus assigned to *Crucibiscutum* sp. cf. *salebrosum*. Other notable *in situ* elements include *N.truitti, F.varolii, F.oblongus, R.orbiculatus, R.planus*, and common/abundant *R.parvidentatum*.

Fullers Earth (*nutfieldiensis* Zone) - A single dissolution-modified assemblage yielded *Crucibiscutum* sp. cf. *salebrosum*, seeming to confirm that this form is not merely reworked in Germany. The only other notable character is the presence of fairly common *R.parvidentatum*.

Discussion

Lithraphidites moray-firthensis, whose last common (= non-reworked?) occurrence Jakubowski (1987) used to define the top of his Early Aptian Zone NLK 9, is notably absent in all this material. Thomsen (1987) and Mutterlose (1991) did not record this distinctive species in any of their onshore material, so it is presumed to be restricted to the *deshayesi* Zone, which is generally of non-nannofossiliferous facies onshore. The only other records of this marker species are from the Danish Central Trough (Thomsen, 1987) and the Heslerton Borehole (this study); in both instances its FO is above the FODs of *F.oblongus* and *F.varolii*, but its LO cannot be constrained due to non-recovery, condensation and barren intervals. Jakubowski (1987) noted that Zone NLK 9 may be difficult to detect in parts of the North Sea, due to condensation of the Lower Aptian.

The FOs of *Radiolithus orbiculatus*, *Radiolithus planus* and *Eprolithus floralis* (= 9 rayed polyclolithaceans with a wide central diaphragm) cannot yet be precisely constrained at Boreal latitudes. Following Thierstein (1971, 1973) numerous authors have used the FO of such forms (generally lumped into either *Eprolithus floralis* or *Eprolithus apertior*) to mark the Lower/Upper Aptian boundary. Jakubowski (1987) placed the FOD of *E.apertior* (= *E.floralis* and *R.orbiculatus*) above the LOD of common *L.moray-firthensis*, in a position approximating the Lower/Upper Aptian boundary. Varol (1992) used the FODs of *R.orbiculatus* and *R.planus* to approximate the Lower/Upper Aptian boundary in the North Sea, and recorded the FO of *E.floralis* slightly later, in the Upper Aptian. However both these studies were based on ditch-cutting material, and their FODs cannot be regarded as well constrained. Thomsen (1987) recorded *"E.apertior"* in the "Fischschiefer" of Helgoland (= upper *forbesi* Zone), but these rare, small and irregular forms were probably aberrant specimens of *F.varolii* (these species are more difficult to differentiate on the SEM, when poorly preserved, since overgrowth results in fusion of the wall elements). Thomsen's oldest definite records of (large and common) *"E.apertior"* are from the *bowerbanki* Zone ("*ewaldi*-Kreide") of Helgoland, and he found this "species" to be very common in the overlying *martinoides* Zone (early Late Aptian). Mutterlose's (1991a) oldest (rare and sporadic) records of *"E.apertior"* are in "Hedbergellen-Mergel" of Hoheneggelsen Well KB 9, which he dated as Lower Aptian. However, Mutterlose did not record this "species" in the middle Aptian of the Rethmar section, so it is likely that his rare earlier records may have been aberrant forms of *F.varolii*. Thus, all the evidence suggests that this important lineage originated in the middle Aptian (upper *bowerbanki* Zone?).

Similarly, the FOs of *Braarudosphaera africana/discula/regularis* cannot yet be accurately constrained. These similar forms are probably conspecific (Lambert, 1986), but

B.africana is particularly distinctive and its FO is a potentially useful event. Perch-Nielsen (1979) used this event, in conjunction with the FO of *"E.floralis"*, to mark the Lower/Upper Aptian boundary. Based on the data compiled herein, the FO of *B.africana* would seem to be in the late Early Aptian (*bowerbanki* Zone?); Mutterlose (1991a) recorded both *B.africana* and *B.regularis* quite consistently in the middle Aptian "*ewaldi*-Mergel" and my own oldest records of this species are from the Gott marls (*nutfieldiensis* Zone) and the Sutterby Marl (undifferentiated Late Aptian). Earlier records of *Braarudosphaera* from elsewhere are probably assignable to *Micrantholithus* (see Systematic Palaeontology).

The FO of common/abundant *Repagulum parvidentatum* is a potentially useful event, which may, in fact, represent the evolutionary origination of this particularly small species. Older LM records (*?R.parvidentatum* was recorded rarely down to the Hauterivian) may belong to a different species - Neocomian forms appear rather simpler on the LM than typical Late Aptian-Albian forms. Thomsen's (1987) oldest SEM record of this species is from an offshore sample located just below the FO of *L.moray-firthensis*. A dramatic influx of *R.parvidentatum* was observed at a similar stratigraphical position in the Heslerton Borehole. Thus, this event might be used to infer an intra-Early Aptian age. *R.parvidentatum* probably remains common/abundant throughout the remainder of the Aptian and the Lower Albian; Jakubowski (1987) and Jeremiah (*in press*) have utilised the top of this acme (LO of common/abundant *R.parvidentatum*) to mark a Middle Albian age.

3.3.10 - Heslerton Borehole 2

(see Fig. 3.8, Fig. 3.9 and Appendix Chart 9)

Nannofossil Preservation - This is poor to moderate through most of the core. Most assemblages from the clays are moderately to strongly etched, while those from the upper chalks and marls are moderately overgrown. The uppermost clays are largely barren. Nevertheless, sufficient nannofossiliferous samples were obtained to enable fairly confident dating of most of this section.

The main part of this core is dated using the sequence of nannofossil datums established above. The remaining, Albian-Cenomanian part of the core is treated separately, and dated by means of the zonation scheme of Jeremiah (*in press*). The Aptian-Albian part of this core is very incomplete; this incompleteness, and the patchy nature of the preservation mean that reliability indices are of restricted use.

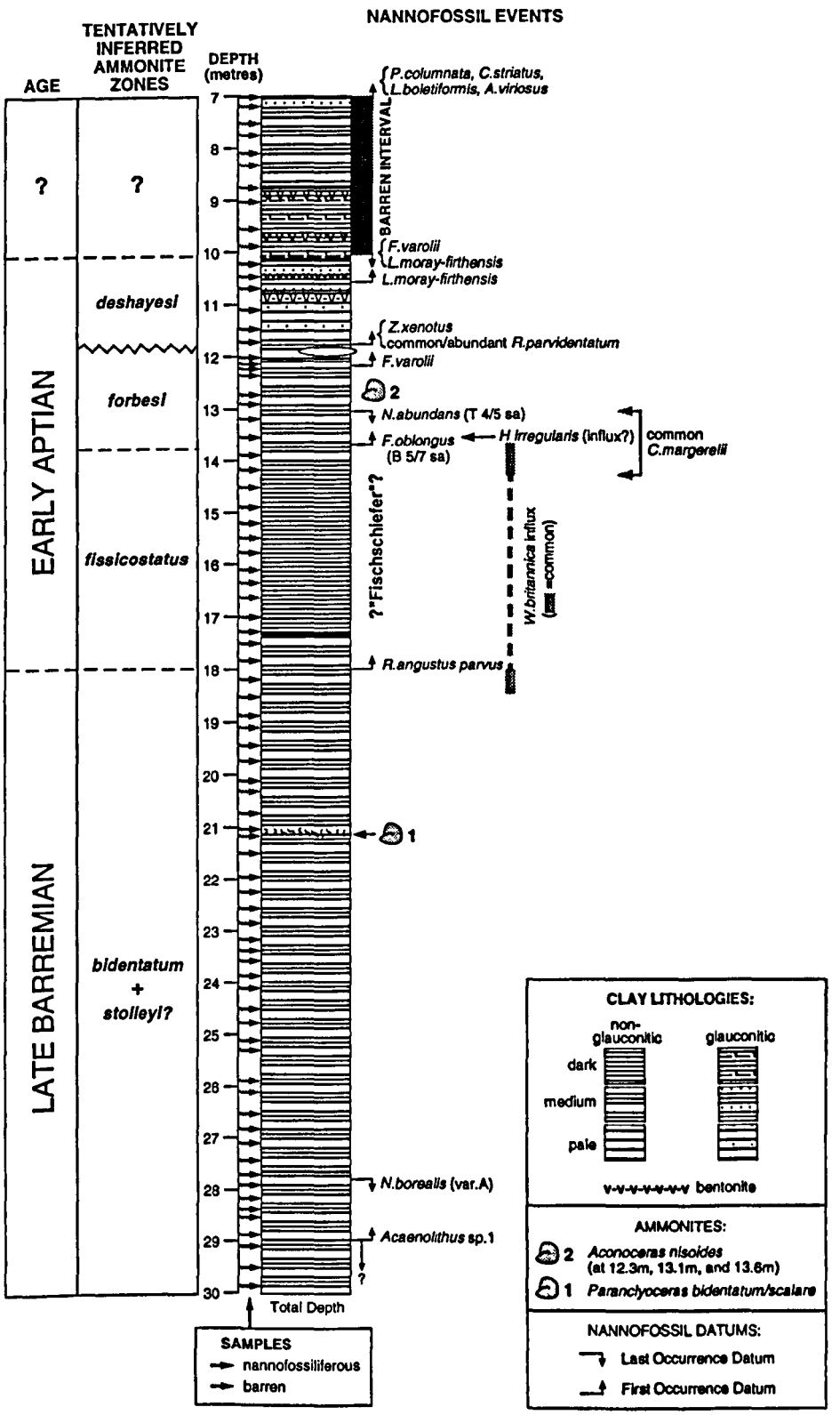


Fig. 3.8 - Summary of the nannofossil biostratigraphy of the lower (Barremian-Aptian) part of the Heslerton Borehole. Ammonite zones are tentatively inferred using the sequence of nannofossil events established in dated outcrop sections.

(1) Uppermost Barremian-Lower Aptian - 30m (T.D.)-c.10m - The dissolution-affected assemblages from the lower part of this core yield *Acaenolithus?* sp.1, *N.abundans* and *N.borealis* var.A; *Z.scutula* is much reduced in abundance relative to the Lower Cement Beds of Speeton or the *germanica* Zone of Gott. This assemblage indicates a Late Barremian (post *denckmanni* Zone) age. These lower clays also yield *Chiastozygus* sp.4 (= *Chiastozygus litterarius?*) and *Tegumentum stradneri*; numerous authors have used the FO of *C.litterarius* to mark the base of the Aptian (most recently Mutterlose, 1991a), but this species remains too ill-defined to be a reliable marker.

Small forms of *R.angustus* (subsp. *parvus*) appear at c.18m; this FO is accompanied by an influx of *W.britannica* (c.5% of a depauperated assemblage). The overlying dark, almost black, pyritic clays yield only sparse nannofloras (with *W.britannica* occasionally common); this horizon is lithologically similar to the "Fischschiefer", but the nannofloral evidence indicates that it is younger than this unit, as described by Thomsen (1987) and Mutterlose (1991a). The occurrence of common *W.britannica*, together with *R.angustus parvus*, and the absence of other, later-appearing forms suggests a late *fissicostatus* Zone age, equivalent to the Perna Beds on the Isle of Wight. This interval also yields very small forms of *Acaenolithus?* (3-4μ long), as observed commonly in the Perna Beds. *C.margerelii* is common for a short interval around the top of this organic-rich unit; this brief, and not particularly dramatic acme may be correlable with the Lower Chale Clay of the Isle of Wight (lower *forbesi* Zone). The FOs of *Flabellites oblongus* and *Hayesites irregularis* were recorded at 13.54m; the former species occurs fairly consistently in the overlying interval (B 5/7 sa), but *H.irregularis* is restricted to a single sample. Thomsen (1987) and Mutterlose (1991a) found that *H.irregularis* was similarly restricted to the "Fischschiefer" in the Danish Central Trough (Well ADDA-2) and Germany (Hoheneggelsen KB 9). This species has a longer, more continuous range at low-latitudes, where its FO has been used to mark the base of the Aptian (Applegate & Bergen, 1988). The FO of *F.varolii*, at 12.13m, confirms that a *forbesi* Zone age has been reached. The presence of fully-flanged, and fairly consistently occurring *N.abundans* up to 12.91m, a level of almost certain Early Aptian age, throws doubt on the use of this species' LO to mark the Barremian-Aptian boundary (Jakubowski, 1987).

A considerable nannofloral turnover, across a sharp lithological contact at 12.07m, indicates a stratigraphical break. *R.parvidentatum*, which is only occasionally (and questionably) recorded in older strata, suddenly becomes common/abundant. *Zeugrhabdotus xenotus*, which was recorded only very rarely and sporadically within the Neocomian (Bergen, 1994, reports the origination of this species in the Early Valanginian of Tethys), also becomes common/abundant above this surface. *Grantarhabdus coronadventis*, which has not previously been recorded below the Lower Albian, was first recorded at this level. *C.angustiforatus*, whose LO Bergen (1994)

reports in the Lower Aptian, has its highest recorded occurrence immediately below (this species was not regarded as having marker potential, and thus has a rather discontinuous range). *F.oblongus*, which both Thomsen (1987) and Mutterlose (1991a) only recorded continuously in the lower part of its range, disappears at this surface (only to reappear in the Lower Albian). The FO of common, definite *L.moray-firthensis* (rather than *L.pseudoquadratus* or forms transitional with *L.moray-firthensis*) at 10.49m suggests a *deshayesi* Zone age (this species has yet to be recorded from any ammonite-dated outcrop material).

The overlying 3m are entirely barren of nannofossils; the next nannofossiliferous sample (at 7.00m) is of Early Albian age. Several bentonitic clays and, in particular, a 10cm thick "bentonite" within this barren interval suggest a Late Aptian age (volcanism was especially prevalent during the Late Aptian; hence the Fullers Earth).

(2a) Lower Albian (+basal Middle Albian?) - 7.00m-c.2.5m - *Prediscosphaera columnata*, at 7.00m, indicates an Albian age (Jeremiah, *pers. comm.*, reports the FO of this species in the Lower Albian). *Acaenolithus viriosus*, whose LO Jeremiah (*in press*) uses to mark the Lower/Middle Albian boundary is present between 7.00-4.03m (5/5 sa); this species has not been observed in the basal Middle Albian clays of Folkstone, and its LO may be intra-Lower Albian, but it provides a good approximation of this substage boundary. This age assignment is substantiated by the presence of *Laguncula boletiformis* and abundant *R.parvidentatum* up to 2.83m (lower Hunstanton Formation). The LO of *L.boletiformis* is in the early Middle Albian *loricatus* ammonite Zone (Crux, 1991; Jeremiah, *in press*). Jakubowski (1987) and Crux (1991) recorded the last consistent common/abundant occurrence of *R.parvidentatum* within the Middle Albian, and Jeremiah (*in press*) records the LO of abundant *R.parvidentatum* synchronously with the LO of *A.viriosus*, at the Lower/Middle Albian boundary. *R.splendens* is abundant throughout this section of core; Jeremiah (*in press*) observes this feature within NAL 1. The FO of *Gaarderella granulifera*, a large and distinctive species only known from the Middle and Upper Albian, was observed at 3.69m; Jeremiah (*in press*) also records the FO of this species in NAL 2. Jeremiah records the FO of *Tranolithus phacelosus* (= *Tranolithus orionatus*) in NAL 2, but I have recorded this species down to 7.00m in this section, well below the LO of *A.viriosus*. This is the least well-constrained part of Jeremiah's zonation, due to a lack of onshore sections spanning the Lower/Middle Albian boundary; this section likely spans this boundary, and demonstrates that several of Jeremiah's Lower/Middle Albian markers have overlapping ranges. Nevertheless most of this section of core can be assigned to the Lower Albian; the basal Middle Albian may also be represented. There follows a major stratigraphical break, with most of the Middle and Upper Albian missing.

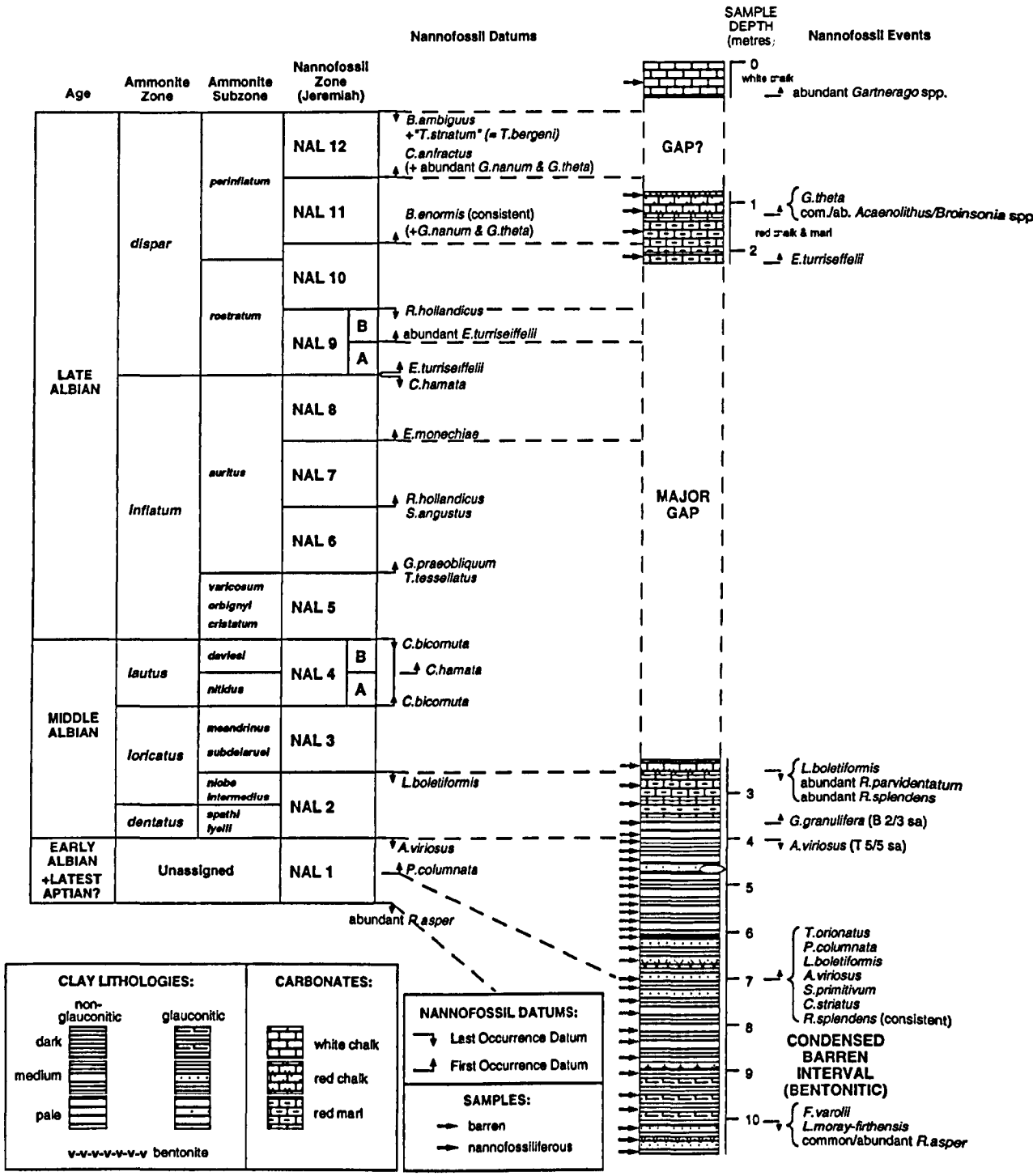


Fig. 3.9 - Nannofossil biostratigraphy of the upper, Albian part of the Heslerton Borehole, utilising the zonation scheme of Jeremiah (*in press*).

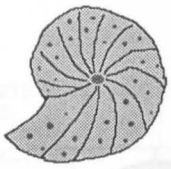
(2b) Upper Albian-Lower Cenomanian - c.2.5m-0.40m (core top) - A major nannofloral turnover across a thin, indurated red chalk horizon (2.50-2.20m), that is barren of nannofossils, indicates a sizeable break. This recrystallised chalk may represent a hardground. *R.parvidentatum*, which is abundant in the underlying beds, is rare or absent above this level, and *L.boletiformis* disappears. The overlying red chalks and marls yield common *E.turriseiffelii*; the absence of *R.hollandicus* and the FOs of *Gartnerago theta* and common *Acaenolithus/Broinsonia* spp. at 1.10m indicate a mid-late *dispar* Zone age (NAL 10/11). *Bukrylithus ambiguus*, whose LO Jeremiah (*in press*) uses to mark the Albian/Cenomanian boundary, is present up to the top of these red carbonates. A single sample from the overlying white chalk yields abundant *Gartnerago theta* and *Gartnerago nanum*, and lacks *B.ambiguus*; this may be very latest Albian or Early Cenomanian in age.

Thus the major stratigraphical break occurs within the Hunstanton Formation (="Red Chalk"), rather than at the facies change between the Speeton Clay and Hunstanton carbonates (which is, anyway, gradational).

3.4 - BIOZONATION SCHEME

In the previous section I have shown that, having achieved a large database of dated outcrop material, core samples can be dated to ammonite zone level through much of the Lower Cretaceous, without recourse to any specific nannofossil zonation. However, while such a "bioevent" approach is very flexible, it is obviously desirable to have a separate nannofossil zonation scheme against which other events may be calibrated. Additionally, it has become apparent that in certain intervals (e.g. the Upper Hauterivian and Lower Barremian) the sequence of nannofloral events is more rigorously defined than the cephalopod zones recognised onshore. Thus, while separate zonal terminologies are applied in Germany and England (e.g. *discofalcatus* Zone = *marginatus* and *variabilis* Zones), these strata are easily and precisely correlated using nannofossils. Previous nannofossil zonations for the Ryazanian-Aptian are limited in their applicability, and a modified scheme is presented below.

The zonation presented herein is largely a compilation of previous schemes, with the various (often seemingly incompatible) events hopefully arranged in sequence. Zones are named after a particularly characteristic taxon and, following the convention with cephalopods, these are abbreviated by dropping the generic epithet. For more convenient reference the zones are labelled BC 1 to BC 22 (BC = Boreal Cretaceous), in ascending order; additional subzones are labelled alphabetically, also in ascending order. Several species are sufficiently short-ranging to enable the definition of total range zones (*M.speetonensis* and *R.antiquus*); *T.septentrionalis* has a total range of comparable duration to an ammonite zone, but this interval can be very confidently subdivided. The remainder of the zones and subzones are defined using discrete F/LODs and acmes. This scheme is only intended to be applicable to the North Sea area, but a number of the events utilised are more widely applicable, and most are probably recognisable in the Barents Sea (the degree of provinciality and possibility of direct inter-regional correlation are discussed further in section 3.5). This zonation is not intended to be rigid - certain zones are fairly tentative, due to incomplete stratigraphical coverage - but it should serve as a framework for the integration of further data. Thus, no "type sections" are quoted; instead I have listed all available **records** of each interval (those recognised in this study are prefixed with an asterisk (*)). It should be emphasised that the **assemblage characteristics** are often more characteristic of a particular interval than the discrete F/LODs used in its definition; previous authors have perhaps concentrated too heavily on the discrete F/LODs of a few recognised "marker" species. The zonation scheme is summarised in Figs. 3.10 and 3.12, and integrated with the palynological zonation of Davey (1979, 1982), also based largely on the Speeton section, in Fig. 3.11.



AGE		AMMONITE ZONE	NANNOFOSSIL ZONE	ZONE NUMBER (& subzones)	NANNOFOSSIL DATUMS
	undifferentiated Early Albian				▲ *P.columnata*
APTIAN	LATE	*jacobi*	*parvidentatum*	BC 22	▼ *F.varolii*
		nutfieldiensis / *martinoides* / *bowerbanki*	*asper*	BC 21	
	EARLY	*deshayesi*	*moray-firthensis*	BC 20	▼ *L.moray-firthensis* / ▲ *L.moray-firthensis*
		forbesi	*varolii*	BC 19	▲ *F.varolii*
		fissicostatus	*britannica*	BC 18	▲ *R.angustus parvus* & re-entry of common *W.britannica*
BARREMIAN	LATE	*bidentatum*	*constans*	BC 17	
		stolleyi	*Acaenolithus?* sp.	BC 16	▼ *N.borealis*
		innexum / *denckmanni*	*scutula*	BC 15	▼ *Z.scutula* acme
	EARLY	*elegans*			▲
		fissicostatum	*borealis*	BC 14	▲ *N.borealis*
		rarocinctum	*abundans*	BC 13	▼ *R.pseudoangustus* / ▲ *N.abundans*
		variabilis	*inequalis*	BC 12	
HAUTERIVIAN	LATE	*marginatus*	*maculosus*	BC 11 B	▼ *C.maculosus*
		gottschei		BC 11 A	▼ very abundant *Z.noeliae*
		speetonensis	*septentrionalis*	BC 10	▼ *T.septentrionalis*
			striatus	BC 9	▼ *E.striatus* / ▲ *T.septentrionalis*
	EARLY	*inversum*	*margerelii*	BC 8 C	▲ *P.plethotretus, P.tayloriae, Z.scutula*
		regale		BC 8 B	
		noricum		BC 8 A	▼ abundant *C.margerelii* / ▼ *R.antiquus*
		amblygonium	*antiquus*	BC 7	▲ *R.antiquus*
			rothii	BC 6	▲ *C.rothii*
VALANG.	LATE	unnamed	*shetlandensis*	BC 5	▼ *T.shetlandensis*
		Dichotomites spp.			
	EARLY	*Polyptychites* spp.	*speetonensis*	BC 4 B	▼ *M.speetonensis* / ▲ *E.windii*
		Paratollia spp.		BC 4 A	▲ *M.speetonensis*
			salebrosum	BC 3 B	▲ *T.shetlandensis*
RYAZANIAN	LATE	*albidum*		BC 3 A	
			arcuatus	BC 2	▼ *S.arcuatus* / ▲ *S.arcuatus*
	undifferentiated		*angustiforatus*	BC 1	▲ *C.angustiforatus*

Fig. 3.10 - Summary of the proposed nannofossil zonation, and integration with ammonite zones.

Fig. 3.11 - Comparison of the proposed nannofossil zonation with the dinoflagellate zonation scheme of Davey (1979, 1982).

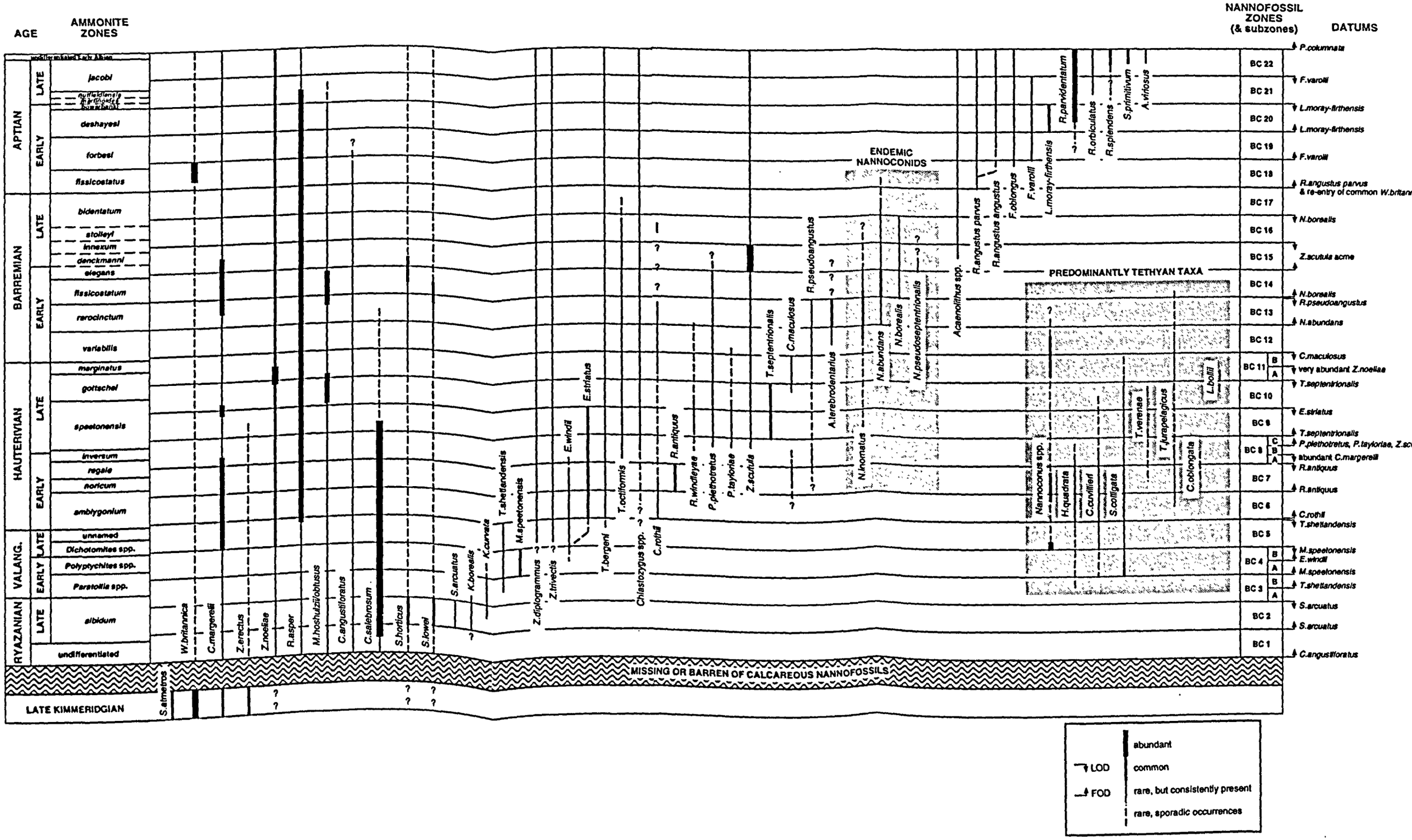


Fig. 3.12 - Ranges of biostratigraphically important nannofossils in the Ryazanian-Aptian of the North Sea area, related to ammonite biostratigraphy and a proposed nannofossil zonation scheme (with zones labelled BC 1 to BC 22).

PAGE

NUMBERING

AS ORIGINAL

Cretarhabdus angustiforatus Zone (BC 1)

Definition - Interval from the first occurrence of *Cretarhabdus angustiforatus* to the first occurrence of *Sollasites arcuatus* (partial range Zone).

Author - Jakubowski, 1987 (*Retecapsa angustiforata* Subzone).

Age - Ryazanian.

Records -
*Speeton: Beds D7E-D6I; c.1m thick; lower *albidum* ammonite Zone; base not seen due to underlying barren interval.
Moray Firth (Jakubowski, 1987).

Remarks - The FO of *C.angustiforatus*, recorded in the Lower Berriasian of Tethys (Bergen, 1994) provides a convenient datum for the definition of a lower boundary. This zone is rarely encountered in the North Sea area, due to non-calcareous facies, and a regional unconformity between the Valhall/Speeton Clay Formation and the underlying (generally non-nannofossiliferous) Kimmeridge Clay Formation. Crux (1989) subdivided this interval using the total range of *Nannoconus* sp. (disks), which he had observed in several offshore wells and found to be restricted to Bed D7B at Speeton. Jakubowski (1987) also recorded these nannoconid disks in the Ryazanian of the Moray Firth (below the LO of *S.arcuatus*), and Varol (1991) recorded the LO of this enigmatic form in the Late Berriasian of Indonesia. In the present study, this form was recorded in Bed D7B, and considerably higher in Bed D4A (Zone BC 3), and thus seems to have been rather longer-ranging than Crux believed. I have also observed this form, rather more commonly, with *S.arcuatus* (possibly caved) in cutting material from an undisclosed North Sea well. Thus *Nannoconus* sp. (disk) is a useful secondary marker for the Upper Ryazanian-?basal Valanginian, but its range is not yet sufficiently well documented to be used as a zonal marker.

Further subdivision of this interval must await the discovery of more complete nannofossiliferous sections. Bralower *et al.* (1989) demonstrated the massive potential for subdivision of the Jurassic-Cretaceous boundary interval in Tethys but, bearing in mind the exceptionally strong provincialism shown by most organisms at this time, it is likely that many of the events recognised therein are diachronous on an inter-regional scale. The Late Kimmeridgian nannofloras from the bottom of Borehole 81/83 share virtually no elements with the earliest Cretaceous nannofloras encountered. LO datums that might be used to divide this interval in the Boreal area include: LO of *Stephanolithion atmetros*, LO of common/abundant *Watznaueria britannica*, LO of common

Zeugrhabdotus erectus, and LO of *Micrascidites?* sp.. A large number of species have there FOs within this interval - the most widely distributed (and thus the most likely to be of use in inter-regional correlation) include *Rotelapillus laffittei*, *Rhagodiscus asper* and the various species of *Cretarhabdus*.

Sollasites arcuatus Zone (BC 2)

Definition - Interval from the first occurrence to the last occurrence of *Sollasites arcuatus* (total range zone).

Author - (Jakubowski, 1987) Crux, 1989.

Age - Late Ryazanian; equivalent to part of the *albidum* ammonite Zone.

Records -
*Speeton: Beds D6I-D6A (?6 sa); c.2-3m thick; upper *albidum* Zone; upper boundary cannot be accurately located due to a barren interval.
*Core 7B: 10.95-10.77m (4 sa); lower boundary not seen, due to underlying barren interval.
*Core 7425/9-U-1: ?65.60-64.28m (2 sa); lower boundary not cored.
*Core 7430/10-U-1 ?: ?41.50m (1 sa); lower boundary not seen due to underlying barren interval.
Moray Firth (Jakubowski, 1987).
Central North Sea (Perch-Nielsen, 1988).

Assemblage characteristics - The nominate taxon, *S.arcuatus*, may be rare within this Zone. The Zone is otherwise characterised by common/abundant *Sollasites* spp. (*S.horticus*, *S.lowei* and indeterminate *Sollasites*) and *C.salebrosum*. A marked influx of *Z.embergeri* in Beds D6I-D6F/G at Speeton may be correlatable offshore (Jakubowski, 1987, also recorded this feature).

Remarks - Within this zone there is a dramatic change in facies from black shale (Kimmeridge Clay) to carbonate (Valhall Formation) throughout much of the North Sea and Barents Sea. Thus the base of the zone often lies in strata barren of calcareous nannofossils.

Cruciblscutum salebrosum Zone (BC 3)

Definition - Interval from the last occurrence of *Sollasites arcuatus* to the first occurrence of *Micrantholithus speetonensis* (interval zone).

Author - Crux, 1989 (= Un-named Zone).

Age - Latest Ryazanian to Early Valanginian; equivalent to the upper part of the *albidum* ammonite Zone and part of the *Paratollia* spp. Zone.

Assemblage characteristics - Dominated by *C.salebrosum*, with conspicuous *Kokia* spp. and, in the upper part, *Triquetrorhabdulus shetlandensis. Micrantholithus brevis*, the precursor of *M.speetonensis*, is a rare element of this and the underlying zone - it is important that this species is distinguished from the later-appearing, fully-developed *M.speetonensis.*

Remarks - This zone is barren of calcareous nannofossils at Speeton, but was identified in a number of offshore cores. The top of the zone is truncated in all three offshore-Norwegian cores. The zone is subdivided using the inception of *T.shetlandensis.*

Subzone BC 3a

Definition - Interval from the last occurrence of *Sollasites arcuatus* to the first occurrence of *Triquetrorhabdulus shetlandensis* (interval subzone).

Author - Rutledge, this study.

Age - Latest Ryazanian (and earliest Valanginian?); equivalent to the upper part of the *albidum* ammonite Zone (and possibly the lower part of the *Paratollia* spp. Zone).

Records -
***Speeton ?**: ?Beds D5-D4B (uppermost *albidum* Zone to upper *Paratollia* spp. Zone); entire interval barren of calcareous nannofossils.
***Core 7B**: 10.77-8.20m (17 sa).
***Core 7425/9-U-1**: 64.00-59.10m (14 sa; mostly impoverished).
***Core 7430/10-U-1**: 41.00-39.57m (4 sa).
?East Shetland Basin (Perch-Nielsen, 1988).

Assemblage characteristics - *C.salebrosum* is the dominant taxon. *Kokia curvata*, *Kokia borealis* and *Nannoconus oviformis* are conspicuous elements within this interval, while *Sollasites* spp. is rare. *K.borealis* has its LO in this subzone (Perch-Nielsen, 1988, recorded this species with or below *S.arcuatus*, in presumably widely-spaced cutting samples). *Nannoconus oviformis* likely has its LO in this interval - this species was only

recorded in Core 7B, but Perch-Nielsen (1988) found it to be restricted to the *S.arcuatus* Zone in the central North Sea.

Remarks - This interval is barren of calcareous nannofossils at Speeton and in Borehole 81/43.

Subzone BC 3b

Definition - Interval from the first occurrence of *Triquetrorhabdulus shetlandensis* to the first occurrence of *Micrantholithus speetonensis* (partial range subzone).

Author - Rutledge, this study.

Age - Early Valanginian; equivalent to part of the *Paratollia* spp. ammonite Zone.

Records -
*Speeton ?: ?upper part of D5-D4B interval (barren of calcareous nannofossils).
*Borehole 81/43 ?: 80.31-69.32m (only 2 reasonably productive samples).
*Core 7B: 8.20-8.00m (3 sa); upper boundary not seen (truncated), but Crux (1989) recorded reworked *M.speetonensis* at the base of the overlying Late Hauterivian section.
*Core 7425/9-U-1: 59.10-57.22m (7 sa); upper boundary not seen (truncated).
*Core 7430/10-U-1: 39.57-39.00m (2 sa); upper boundary not seen (truncated).
?Northern North Sea: Perch-Nielsen (1988) recorded the FO of *T.shetlandensis* in Jakubowski's Zone NLK 18, between the LOs of *S.arcuatus* and *M.speetonensis*, but could not place this event relative to the FO of *M.speetonensis* due to the limitations imposed by cutting samples.

Assemblage characteristics - Dominated by *C.salebrosum*, with conspicuous *T.shetlandensis* and *K.curvata*. The latter species has only been recorded in the northern North-Sea and Barents Sea, and may not have ranged into the southern North Sea.

Micrantholithus speetonensis Zone (BC 4)

Definition - Interval from the first occurrence to the last occurrence of *Micrantholithus speetonensis* (total range Zone).

Author - Crux, 1989.

Age - Early Valanginian; equivalent to the upper part of the *Paratollia* spp. ammonite Zone and the whole of the *Polyptychites* spp. Zone.

Remarks - This zone is subdivided using the FO of *Eiffellithus windii*; this is an important, inter-regionally correlatable event which is, however, rather difficult to pin-point in the Boreal area due to condensation of mid-late Valanginian sections.

Subzone BC 4a

Definition - Interval from the first occurrence of *Micrantholithus speetonensis* to the first occurrence of *Eiffellithus windii* (partial range Zone).

Author - Rutledge, this study.

Age - Early Valanginian; equivalent to the upper *Paratollia* spp. to lower *Polyptychites* spp. ammonite Zones.

Records -
***Speeton**: Beds D4A-D3D; at least 1m thick; upper *Paratollia* spp. Zone to lower *Polyptychites* spp. Zone; lower boundary overlying barren interval; upper boundary not very confidently fixed due to the extreme rarity of *?Eiffellithus windii.*
***Borehole 81/43**: 69.32-66.28m (4 sa); upper boundary not seen (truncated).
S.E. France (Angles): Beds 250-258 (interpolated from Bergen, 1994); both lower and upper boundaries identified.

Assemblage characteristics - Assemblages are dominated by *C.salebrosum*, with conspicuous *M.speetonensis*, *T.shetlandensis* and *Cyclagelosphaera brezae. Cruciellipsis cuvillieri* and *Speetonia colligata* were first recorded within this interval (the latter species abundantly); these species are late entrants to the Boreal area, and there sudden *en masse* appearance probably reflects the opening of a marine connection to the south.

Remarks - The lack of complete, nannofossiliferous mid-late Valanginian sections means that this interval must be zoned largely by inference from other worker's data. Jakubowski (1987) recorded *"Chiastozygus striatus"* (= *Eiffellithus striatus/windii*) in Bed D3A at Speeton. In this study, a single large, indeterminate specimen of *Eiffellithus* (lacking its central diagonal cross) was recorded in Bed D3C. These Early Valanginian records almost certainly belong to *Eiffellithus windii*, which Bergen (1994) reports to originate in the Early Valanginian *campylotoxum* ammonite Zone of S.E. France, where its FOD lies within the (more limited?) range of *M.speetonensis*. Bergen also records this FOD at a similar level (without *M.speetonensis*) at DSDP Site 534, but reports (*pers. comm.*) that *E.windii* is extremely rare towards the base of its range in this section. *Eiffellithus striatus* (=*"Tegumentum tripes"* in Mutterlose, 1991a) did not, apparently,

originate until the Late Valanginian in both Tethys (Applegate & Bergen, 1988, redated; Bergen, 1994) and the Boreal area (Mutterlose, 1991a). Mutterlose (1991a) recorded *"Tegumentum striatum"* (= composite concept including *E.windii*) down to the base of the Upper Valanginian *Dichotomites* beds in Germany, but the underlying Lower Valanginian strata were barren of calcareous nannofossils. In this study, *E.windii* was recorded in the only Late Valanginian sample obtained from Germany (*Dichotomites crassus* Zone), and in ammonite-dated middle Valanginian strata from Borehole 81/43. The lack of overlap in the ranges of *M.speetonensis* and *E.windii* in Borehole 81/43 can be explained by a stratigraphical break at c.66m (this is reflected by a microfaunal turnover which Lott *et al.*, 1986, mistakenly took to indicate a disconformable Valanginian/Hauterivian boundary). I have also observed coexisting *M.speetonensis* and *E.windii* in a sample from Tunisia (see Records under BC 4b). Thus, all the evidence suggests that the ranges of *M.speetonensis* and *E.windii* must overlap in the Boreal area, and the tentative zone that Crux (1989) proposed to cover the apparent separation between the ranges of *M.speetonensis* and *"Tegumentum striatum"* does not exist. Bearing in mind the rarity of *E.windii* towards the bottom of its range, and the relative scarcity of the evidence, this interval is given only subzonal status.

Subzone BC 4b

Definition - Interval from the first occurrence of *Eiffellithus windii* to the last occurrence of *Micrantholithus speetonensis* (concurrent range subzone).

Author - Rutledge, this study.

Age - Late Early Valanginian; equivalent to the upper part of the *Polyptychites* spp. ammonite Zone, and possibly the basal part of the *Dichotomites* spp. Zone.

Records -

*Speeton: Beds D3C-D2E; c.3.3m thick; upper *Polyptychites* spp. Zone; lower boundary not very confidently fixed due to the extreme rarity of *E.windii*; upper boundary may be truncated.

S.E. France (Angles): Beds 258-261 (interpolated from Bergen, 1994); upper boundary is likely older than in the Boreal area, since *M.speetonensis* probably has a more limited range outside the Boreal area.

*Tunisia: a single Early Valanginian sample (dated here) yielded both *M.speetonensis* and *E.windii*; other biostratigraphically important taxa present include *C.oblongata*, *R.parallelus*, and *Z.diplogrammus*, all of which first appear in the Early Valanginian of low-latitudes (Bergen, 1994).

Assemblage characteristics - As for BC 4a, but with the addition of *Eiffellithus windii*. Based on the limited evidence from the Speeton section, *Speetonia colligata* is probably common throughout this interval.

Remarks - (See remarks under BC 4a) - Due to regional unconformities and barren intervals this interval has not yet been confidently identified in the Boreal area. Investigation of thicker, nannofossiliferous Valanginian sections should enable this interval to be proven.

Triquetrorhabdulus shetlandensis Zone (BC 5)

Definition - Interval from the last occurrence of *Micrantholithus speetonensis* to the first occurrence of *Conusphaera rothii* (or the last occurrence of *Triquetrorhabdulus shetlandensis*).

Author - Rutledge, this study.

Age - Late Valanginian (+earliest Hauterivian?); equivalent to the *Dichotomites* spp. to ?*amblygonium* ammonite Zones.

Records -
***Speeton ?** - Bed D2D (1 sa); remanié horizon containing derived mid-late Valanginian ammonites, and an *in situ* macrofauna of *amblygonium* Zone age. Several specimens of *T.shetlandensis* were recorded from this horizon; these may be have been reworked from anywhere within the mid-upper Valanginian.
***Borehole 81/43**: 65.68-63.99m (5 sa); the ammonite *K.heteroptychum* at 64.46m indicates a "middle" Valanginian age (?lower *Dichotomites* spp. ammonite Zone); lower boundary disconformable, upper boundary truncated.

Assemblage characteristics - Common/abundant *C.salebrosum* and *C.margerelii*, with common *E.windii* and rare but conspicuous *T.shetlandensis*. *Calculites?* sp.1 and *Nannoconus* spp. are occasionally abundant. *Z.diplogrammus* and *Z.trivectis* are first recorded in this interval, but may have originated in the upper, unseen part of BC 4. The FOs of *Percivalia fenestrata* and *Assipetra infracretacea* were recorded in this interval, but these species originated much earlier in Tethys (Bralower *et al.*, 1989; Bergen, 1994). *Eiffellithus striatus* (="*Tegumentum tripes*" in Mutterlose, 1991a) originates within this interval, but is gradational with *E.windii*.

Remarks - Due to the very limited amount of Upper Valanginian material available in this study this rather long interval cannot yet be satisfactorily subdivided. Crux (1989)

tentatively subdivided this interval using the FO of *"Tegumentum striatum"* (= *Eiffellithus* spp. + *Tegumentum bergeni*) but, as discussed above, the FO of *E.windii* must lie within the range of *M.speetonensis*. Having studied thick Upper Valanginian sequences in Germany, Mutterlose (1991a) subdivided this interval using the FO of *Conusphaera rothii* (in the uppermost *Dichotomites* Beds) and several *Nannoconus* acmes; however, judging from his range charts, the COR of *C.rothii* is very low towards its base, and this may not be a reliable datum. Additionally, this species has been reported down to the Lower Tithonian in the Tethyan area (Thierstein, 1971), although these older records may belong to *Conusphaera mexicana*. The oldest Boreal records of *C.rothii* in this study are from the basal Hauterivian of Germany (Moorberg), and Bed D2D at Speeton (also basal Hauterivian) - the same bed in which the last (possibly reworked) *T.shetlandensis* was recorded. In the present study, *T.shetlandensis* was proven to range considerably higher than *M.speetonensis*, into the Upper Valanginian or basal Hauterivian (unfortunately neither Crux nor Mutterlose recognised this species). Thus two alternative datums (FO of *C.rothii* and LO of *T.shetlandensis*) are offered; further study of more complete Valanginian sequences should enable proper sequencing of these events but, for the moment, it is felt that they are sufficiently close to be complimentary.

Applegate & Bergen (1988) used the FO of *Eiffellithus striatus* to define a subzonal boundary approximating the base of the Hauterivian. Bergen (1994) records this event in the Upper Valanginian of S.E. France, and Mutterlose (1991a) recorded the FO of the synonymous *Tegumentum tripes* in the Upper Valanginian of Germany, shortly below the FO of *C.rothii*. However, in this study *E.striatus* was recorded in the mid-Valanginian (ammonite-dated) of Borehole 81/43, and forms transitional between *E.windii* and *E.striatus* were observed in a mid-late Valanginian sample from Germany. There is no doubt that *E.windii* is the dominant form of *Eiffellithus* in the mid-late Valanginian, and that it is largely superseded by *E.striatus* in the latest Valanginian, but exact placement of the FOD of *E.striatus* is problematical. Again, further investigation of thicker Valanginian sequences may clarify this point.

Conusphaera rothii Zone (BC 6)

Definition - Interval from the first occurrence of *Conusphaera rothii* (or the last occurrence of *Triquetrorhabdulus shetlandensis*) to the first occurrence of *Radiolithus antiquus* (partial range Zone).

Author - Mutterlose, 1991, emend. this study.

Age - ?Latest Valanginian to earliest Hauterivian; equivalent to the *?ivanovi* to mid-*amblygonium* ammonite Zones.

Records -
***Speeton:** Beds D2D-D2B (2 sa); lower *amblygonium* Zone; base disconformable.
***Germany (Moorberg):** Bed 101 (verified by Crux, 1989 and Mutterlose, 1991a); base not seen.
Germany (Wiedensahl 2 well): Beds 34,5-1,5 (after Mutterlose, 1991a); top not seen.
Germany (Niedermehnen 3) ?: Beds 71-99 (after Mutterlose, 1991a); *amblygonium* Zone.
***Borehole 81/43 ?:** 63.60m (1 sa); base disconformable.
C.rothii was not recorded this low in the latter two sections, but the zone is taken to lie below the range of *R.antiquus* (and above that of *T.shetlandensis*, in Borehole 81/43).

Assemblage characteristics - Abundant *C.margerelii*, with common *E.striatus*, rather less common *E.windii*, and rare/few *C.rothii*. *Cyclagelosphaera brezae* and *Stradnerlithus silvaradius* may be conspicuous within this interval.

Remarks - This interval is often highly condensed, and its base often disconformable.

Radiolithus antiquus Zone (BC 7)

Definition - Interval from the first occurrence to the last occurrence of *Radiolithus antiquus* (total range Zone).

Author - (Crux, 1989) Mutterlose, 1991.

Age - Early Hauterivian; equivalent to the upper *amblygonium* to lower *regale* ammonite Zones.

Records -
***Speeton:** Beds D2A-C9D(lower); c.4m thick; *amblygonium* to *regale* Zones.
***Germany (Moorberg):** Beds 101-80 (after Crux, 1989; confirmed this study); c.21m thick; *amblygonium* to *regale* Zones.
Germany (Niedermehnen 3): Bed 101 (after Mutterlose, 1991a); *amblygonium* Zone; top not seen.
***Borehole 81/43:** 63.02m (1 sa); entire interval highly condensed.
***Core 7425/9-U-1:** 56.92m (1 sa); entire interval highly condensed.

Assemblage characteristics - Very abundant to abundant *C.margerelii*, with common/abundant *C.salebrosum*, common *E.striatus* and subordinate *E.windii*. *R.antiquus* is rare to abundant. *Tegumentum bergeni* is also characteristic of this zone; fully-developed, regular *Tegumentum octiformis* did not apparently develop until later. *Stradnerlithus silvaradius* and *Calculites?* sp.1 may be locally abundant. This zone is characterised by strong Tethyan influence - *Cruciellipsis cuvillieri* and *Calcicalathina oblongata*, in particular, may be relatively common.

Remarks - Crux (1989) could not confidently place the FO of *R.antiquus*, due to a lack of data from the Upper Valanginian, but Mutterlose (1991a) demonstrated that this species originates in the Early Hauterivian *amblygonium* Zone. Both these authors recorded quite discontinuous ranges for this species; in the present study it was observed to have a perfectly continuous distribution (COR = 100%) throughout its, albeit condensed, range (but it does vary greatly in abundance from sample to sample). This interval is often extremely condensed. Closer examination of the thicker German sections may allow further subdivision.

Cyclagelosphaera margerelii Zone (BC 8)

Definition - Interval from the last occurrence of *Radiolithus antiquus* to the first occurrence of *Tegulalithus septentrionalis* (interval zone).

Author - Mutterlose, 1991, emend. this study.

Age - Mid-Hauterivian; equivalent to the upper *regale* to lower *speetonensis* ammonite Zones.

Assemblage characteristics - *E.striatus* is a common and conspicuous element throughout this zone, while *C.salebrosum* is common/abundant. *C.margerelii* is abundant in the lower part of this Zone, and the top of this long-term acme is a useful event. *Perissocyclus plethotretus*, *Perissocyclus taylorlae*, *Rucinolithus windleyae* and *Zeugrhabdotus scutula* first appear towards the top of this zone. There appear to be no extinctions during this interval, other than the premature, regional disappearances of *Helenea quadrata*, *Calcicalathina oblongata* and *Stradnerlithus silvaradius*.

Remarks - Jakubowski (1987) and Crux (1989) subdivided this interval using the LO of *Corollithion silvaradion* (= *Stradnerlithus silvaradius*). In this study, *S.silvaradius* was found to be extremely rare in all but the basal Hauterivian of Germany, but was recorded sporadically up to about the same level as Crux (*inversum* Zone, at Speeton). Both Crux and Mutterlose (1991) recorded *S.silvaradius* continuously through much of

the Early Hauterivian of Germany (Moorberg), but Crux's records of this species at Speeton are, as herein, sporadic. In any case, Bergen (1994) records this species up to the Late Hauterivian of France and DSDP Site 534, and it was originally described (Wise & Wind, 1977) from the Aptian of the Falkland Plateau. Bearing in mind these various uncertainties, this species is not a good choice for a zonal marker (it is anyway a small and inconspicuous form). This interval is subdivided here using the top of a *C.margerelii* acme, and a number of approximately synchronous FOs. These events are perhaps not ideally well constrained, and are only used as subzonal markers.

Subzone BC 8a

Definition - Interval from the last occurrence of *Radiolithus antiquus* to the last consistent occurrence of abundant (approximately 10% of the assemblage) *Cyclagelosphaera margerelii* (partial range subzone).

Author - Rutledge, this study.

Age - Lower Hauterivian; equivalent to part of the *regale* ammonite Zone.

Records -
***Speeton**: Beds C9D(mid)-C8B(lower); 7 sa; c.3m thick; *regale* Zone.
***Borehole 81/43 ?**: 62.38-61.84m (2 sa); highly condensed.
Germany (Moorberg): Beds 80-73(lower); c.4m thick; *regale* Zone (after Crux, 1989).

Assemblage characteristics - Abundant *C.margerelii*, with common *E.striatus*, rare *E.windii*, and variable quantities of *C.salebrosum*. Fully-developed, regularly-formed *Tegumentum octiformis* first appears in this interval. As in BC7, there is considerable Tethyan influence, with taxa such as *Cruciellipsis cuvillieri* relatively common. A brief influx of *Diloma galiciense* is correlatable between Speeton and Borehole 81/43.

Remarks - *C.margerelii* is abundant throughout the Upper Valanginian (Mutterlose, 1991) and much of the Lower Hauterivian, and the top of this long-term acme is an important event. This major species forms another, relatively brief acme in the Upper Hauterivian, and a long-term acme in the mid-Barremian, but is relatively rare in the intervening strata. These acme events seem to be correlatable on a basin-wide scale (certainly between England, Germany and the northern North Sea). This interval is often condensed (e.g. in Borehole 81/43) - thus Mutterlose (1991a) recorded the LOs of *R.antiquus* and abundant *C.margerelii* as synchronous events - but is likely to be more

easily identified in thicker, offshore sequences (Varol, 1991 and *pers. comm.*, records this event above the LO of *R.antiquus* in North Sea well material).

Subzone BC 8b

Definition - Interval from the last consistent occurrence of abundant *Cyclagelosphaera margerelii* to the first occurrence of *Perissocyclus plethotretus* (and/or *Perissocyclus tayloriae* and/or *Zeugrhabdotus scutula*) (interval subzone).

Author - Rutledge, this study.

Age - Early-mid Hauterivian; equivalent to the upper *regale* to uppermost *inversum* ammonite Zones.

Records -
*Speeton: Beds C8B(lower)-C7A(upper); 29 sa; c.5m thick; upper *regale* Zone to uppermost *inversum* Zone.
*Borehole 81/43: 61.36-56.78m (13 sa).
*Core 7425/9-U-1: ?38.55-?37.00m; base not seen (disconformable).
*Germany ?: cannot be identified due to insufficient material and the different species concepts used by Crux (1989) and Mutterlose (1991a); nevertheless, the oldest records of *P.plethotretus*, *P.tayloriae* and *Z.scutula* in the *staffi* Zone of Moorberg are consistent with the existence of this interval in the underlying, unsampled section.

Assemblage characteristics - *E.striatus* is a common and conspicuous element and *C.salebrosum* is common/abundant. *C.margerelii* is much reduced in abundance compared to the underlying subzone - it is still common, but forms <3% of assemblages. *Rucinolithus windleyae* first appears towards the top of this interval.

Remarks - The three FOs given to mark the top of this interval cannot yet be satisfactorily sequenced, but are sufficiently close to be complimentary. The FO of *P.plethotretus* is given precedence, since this species seems the most widely distributed within the Boreal area (it is the only one recorded from the Barents Sea). Taylor (1978, 1982) recorded the FO of large, birefingent-strutted forms of *Perissocyclus* above the unexposed C4-C5 interval at Speeton, assigning them to *"Dodekapodorhabdus noelii"*, but could not properly place this event due to a lack of Upper Hauterivian material. Crux (1989) included small forms of *Perissocyclus*, with non-birefringent central struts, in his broader concept of *P.plethotretus*, thus giving this species a much earlier FO. The problems arising from different concepts of these three marker species are discussed in depth in the Systematic Palaeontology section.

Subzone BC 8c

Definition - Interval from the first occurrence of *Perissocyclus plethotretus* (and/or *Perissocyclus tayloriae* and/or *Zeugrhabdotus scutula*) to the first occurrence of *Tegulalithus septentrionalis* (partial range subzone).

Author - Rutledge, this study.

Age - Mid-Hauterivian; equivalent to the uppermost *inversum* and lower *speetonensis/staffi* ammonite Zones.

Records -
***Speeton:** Beds C7A(upper)-C5L (4 sa); at least 5m thick; uppermost *inversum* to lower *speetonensis* Zones; upper boundary not seen (in unexposed section).
***Borehole 81/43:** 56.78-52.71m (8 sa).
***Core 7430/10-U-1:** ?37.00-36.10m (?3 sa); upper boundary not seen (truncated).
?Nettleton, England: Jakubowski (unpublished) recorded *"Dodekapodorhabdus noelii"* (= *P.plethotretus/tayloriae?*) in the *inversum* Zone of the Lower Tealby Clay, several metres below the FO of *T.septentrionalis.*
?Germany: not yet proven due to insufficient samples and the different species concepts of previous authors (see also previous subzone).

Assemblage characteristics - Common/abundant *C.salebrosum*, common *E.striatus*, with rare to common (but conspicuous) *P.plethotretus*, *P.tayloriae* and *Z.scutula*. *Assipetra infracretacea* is common/abundant throughout this interval. The combination of large, birefringent-strutted forms of *Perissocyclus* with *E.striatus* and common/abundant *C.salebrosum* (without *T.septentrionalis*) is characteristic of this interval.

Remarks - See remarks under previous Subzone, and the emended taxonomic descriptions of *P.plethotretus* and *P.tayloriae.*

Eiffellithus striatus Zone (BC 9)

Definition - Interval from the first occurrence of *Tegulalithus septentrionalis* to the last occurrence of *Eiffellithus striatus* (concurrent range zone).

Author - Rutledge, this study.

Age - Late Hauterivian; equivalent to part of the *speetonensis/staffi* ammonite Zone.

Records -
*Speeton ?: lies within an unexposed interval (Beds C5K-C4D; *speetonensis-gottschei* Zones); Crux (1989) recorded *T.septentrionalis* commonly in a single, unplaced sample from this interval; my highest record of *E.striatus* is immediately below this sampling gap.
*Borehole 81/43: 52.23-43.24m (20 sa).
*Germany (Moorberg): Beds 71-?66(upper); lower limit from Mutterlose (1991), upper limit this study (limited by sample density); 2-4m thick; *staffi* Zone.
*Core 7425/9-U-1: 55.50m; condensed into a single sample interval.
Danish Central Trough: Thomsen (1987) recorded the LO of *Chiastozygus striatus* (= *E.striatus*) within the range of *T.septentrionalis* in Well 1-1.

Assemblage characteristics - *T.septentrionalis* is common/abundant throughout this interval, and its sudden *en masse* appearance is an excellent datum. *Assipetra infracretacea* is common/abundant and *?Repagulum parvidentatum* common throughout much of the Zone. Large, multiperforate podorhabdids are conspicuous throughout; *P.tayloriae* is virtually confined to this zone and the underlying BC 8c. *Z.scutula* is a rare but characteristic element. *Calculites burnettiae* is common/abundant within this zone; a very simple, unornamented variety (var.B) seems entirely restricted to this interval. There is a dramatic and terminal reduction in the abundance of *C.salebrosum* within the lower part of this zone which may, in fact, represent the extinction of this species; later, rare records are likely reworked or belong to another, similar species (*Crucibiscutum ?pinnatus* or *Crucibiscutum hayi*). *Cretarhabdus inequalis* first appears in this interval, but is rare towards the base of its range. The LOs of *Cruciellipsis cuvillieri* and *Zeugrhabdotus erectus* were recorded within this interval, but these Tethyan-derived species are extremely rare in their upper ranges and their LOs are not representative of their true extinction levels, as recorded at low-latitudes (Bralower, 1991, recorded rare and sporadic occurrences of *C.cuvillieri* above the LO of *E.striatus* in Borehole 81/43). Jakubowski (1987) used the LO of *C.cuvillieri* to subdivide the range of *T.septentrionalis*, but this species is too rare, and its LO likely to be strongly diachronous within the Boreal area. *E.striatus*, however, is common throughout its range (COR = c.100%), and its LO provides a very reliable datum that is likely correlatable world-wide. *C.margerelii* forms a brief acme at about the extinction level of *E.striatus*, that is correlatable between Borehole 81/43 and Germany.

Remarks - This interval could be subdivided using the LO of common/abundant *C.salebrosum*, which may represent the extinction of this species. However this event is not yet well constrained by precise identification in a number of uncondensed sections, and its position may have been influenced by reworking. Nevertheless, this remains a

very significant high-latitude event in both northern and southern hemispheres (Mutterlose, 1992c, recognised this event at ODP Sites 765 and 766, off N.W. Australia), although its synchroneity in northern and southern hemispheres is not yet established. Jakubowski (1987) used the LO of (rare) *C.salebrosum* to mark the top of his Early Barremian NLK 13 Zone, but these Barremian forms may belong to a different species (*Crucibiscutum ?pinnatus* - see discussion in Systematic Palaeontology).

Tegulalithus septentrionalis Zone (BC 10)

Definition - Interval from the last occurrence of *Eiffellithus striatus* to the last occurrence of *Tegulalithus septentrionalis* (partial range zone).

Author - Rutledge, this study.

Age - Late Hauterivian; equivalent to the upper part of the *speetonensis/staffi* Zone and the lower part of the *gottschei* Zone.

Records -
(unexposed at Speeton - see Records under BC 10)
***Borehole 81/43**: 42.90-36.28m (15 sa).
***Germany (Moorberg)**: Beds ?66-41; upper and lower limits this study (lower imprecise due to sample density); 7-8m thick; upper *staffi* to lower *gottschei* Zones; higher records of *T.septentrionalis* by Crux (1989) are probably reworked.
***Core 7425/9-U-1**: 55.20m; condensed into a single sample interval; top may be truncated.
***Core 7B**: missing, but Crux (1989) recorded *T.septentrionalis* at 7.35m, almost certainly reworked from the missing section; *E.striatus* was not recorded in this section.
Danish Central Trough (Well 1-1): Thomsen (1987).

Assemblage characteristics - As for BC 9, but without *E.striatus*. *Calculites* spp. and *Crucibiscutum* spp. are rare in this zone. *Micrantholithus* spp. becomes abundant towards the top of the interval. *Clepsilithus maculosus* reappears just below the LO of *T.septentrionalis*, after a long absence from the area; Jakubowski (unpublished) recorded the appearance (re-entry) of *"Stradnerlithus comptus"* (= *C.maculosus*) at a similar level at Nettleton. *Rucinolithus windleyae* is occasionally common/abundant. Bralower (1991) recorded the last (very rare) occurrence of *C.cuvillieri* in this interval. The highest occurrence of *Tubodiscus verenae* was recorded in this zone; this species is rare at Boreal latitudes, and of no real marker potential, but these late occurrences are significant because the species' LO has previously been used to mark the top of the Valanginian (e.g. Bralower, 1991).

Remarks - Jakubowski (1987) and Crux (1989) recorded an abrupt and substantial reduction in the abundance of *T.septentrionalis* towards the top of its range, which they extended into the Early Barremian. Mutterlose (1991) recorded a single isolated occurrence of this species in the *discofalcatus* Zone, well above its continuous range, and on this basis extended its range to the base of the Barremian. This is not substantiated in the present study, and the rare Early Barremian records of these authors are believed to have been reworked. *T.septentrionalis* is common/abundant throughout its range in the studied sections, and its LO is abrupt and final (Thomsen, 1987, recorded a similarly abrupt extinction). Crux used the re-entry of *T.septentrionalis* to mark the base of his middle Barremian *Z.sisyphus* Zone, but these records belong to the light-microscopically similar *Nannoconus pseudoseptentrionalis*. Similarly, Mutterlose and Harding's (1987) middle Barremian records of *T.septentrionalis* are assignable to *Nannoconus*.

Clepsilithus maculosus Zone (BC 11)

Definition - Interval from the last occurrence of *Tegulalithus septentrionalis* to the last occurrence of *Clepsilithus maculosus* (partial range zone).

Author - Crux, 1989 (= *Stradnerlithus comptus* Zone), emend. this study.

Age - Late Hauterivian (and very earliest Barremian?); equivalent to the upper part of the *gottschei* ammonite Zone, the whole of the *marginatus* Zone, and the basal part of the *variabilis* Zone. The upper boundary of this zone is within a few centimetres of the Hauterivian/Barremian boundary, as currently defined at Speeton.

Records -

*Speeton: Beds C4C-C2C(lower); 15 sa; *gottschei* to basal *variabilis* Zones; c.5m thick; lower boundary not seen due to non-exposure; upper boundary may be very slightly higher - Crux (1989) recorded the LO of *"Stradnerlithus comptus"* (= *C.maculosus*) in Bed C2B but this is not substantiated, despite very close sampling of this horizon.

*Borehole 81/43: 35.80-22.90m (27 sa); both lower and upper boundaries seen.

*Core 7B: 7.35-4.50m (using additional occurrences from Crux, 1989); 14 sa; lower boundary not seen (disconformable), but Crux (1989) recorded rare *T.septentrionalis* (presumably reworked) at the base of this section; upper boundary not cored.

Moray Firth: Jakubowski (1987) recorded the LO of *"S.comptus"* shortly above the LOs of *T.septentrionalis* and *Speetonia colligata*.

?Nettleton: Jakubowski (unpublished) recorded the re-entry of *"S.comptus"* in the uppermost part of *T.septentrionalis'* range (uppermost Lower Tealby Clay); thus this zone probably exists in the overlying (unsampled) basal Tealby Limestone.

Assemblage composition - *C.maculosus*, which is entirely absent from North Sea sections during the middle Hauterivian, occurs consistently, and often commonly, throughout this interval. *P.plethotretus* and *Z.scutula* are conspicuous throughout. *Micrantholithus* spp. is very abundant towards the base of the interval - Jakubowski (1987) also recorded this feature in the Moray Firth Basin. The diminutive *Zeugrhabdotus noeliae* is extremely abundant throughout the lower half of this zone - this long-term, continuous acme seems to be correlatable basin-wide, and is used to subdivide the interval.

Remarks - This zone has not yet been identified in Germany - neither Crux (1989) nor Mutterlose (1991a) recorded *C.maculosus* in the Upper Hauterivian of Germany. It is anticipated that this species should occur in the lower part of the *discofalcatus* ammonite Zone (= that part equivalent to the *marginatus* Zone of Speeton); the lack of records may be explained by non-exposure of the lower part of this cephalopod zone. This seems to be the case at the Frielingen and Gott sections; Mutterlose (1991a) places the lowest beds exposed at Gott in the *discofalcatus* Zone, not the *gottschei* Zone as recorded by Mutterlose (1984) and followed by Crux (1989). The junction between the *gottschei* and *discofalcatus* Zones is exposed at Moorberg, and was sampled by Mutterlose (1991) who did not record *"S.comptus"*, but there may be a non-sequence in this section, with the lower part of the *discofalcatus* Zone missing. Alternatively, this section may not have been sampled closely enough to detect this nannofloral zone. Whatever the case, it seems that the latest Hauterivian to earliest Barremian interval is more easily correlated between Britain and Germany using nannofossils; the ammonite and belemnite zonal boundaries and even the Hauterivian/Barremian boundary are by no means clear cut, and have been subject to a certain amount of juggling in recent literature.

Subzone BC 11a

Definition - Interval from the last occurrence of *Tegulalithus septentrionalis* to the last consistent occurrence of very abundant (>20% of assemblage) *Zeugrhabdotus noeliae*, within the range of *Clepsilithus maculosus* (partial range subzone).

Author - Rutledge, this study.

Age - Late Hauterivian; equivalent to the upper part of the *gottschei* ammonite Zone. The upper boundary of this subzone is coincident with that of the *gottschei* Zone, as defined at Speeton.

Records -
*Speeton: Beds C4C-C4A; 4 sa; upper *gottschei* Zone; c.1.3m thick; lower boundary unexposed.
*Borehole 81/43: 35.80-28.35m (18 sa); both lower and upper boundaries seen.
*Core 7B: 7.35-5.10m (9 sa); lower boundary not seen (disconformable).
*Moorberg ?: a single sample from the *gottschei* Zone, above the LO of *T.septentrionalis*, yielded very abundant *Z.noeliae*, but not *C.maculosus*.

Assemblage characteristics - Numerically dominated by *Z.noeliae*, which constitutes 20-50% (generally 30-40%) of assemblages; with >15 individuals in an average field of view. *C.maculosus* is an essential component. *Micrantholithus* spp. is very abundant in the lower part of this interval.

Remarks - *Z.noeliae* suffers sudden, and dramatic depletion at the top of this interval; it is still common/abundant throughout the remainder of the range of *C.maculosus*, but does not dominate assemblages (constituting <15%; generally much less). This LOD may not be easily recognisable in ditch-cutting material, since *Z.noeliae* is occasionally very abundant in the overlying zone; the *Micrantholithus* spp. acme (also noted by Jakubowski, 1987) may be a more easily utilised event.

Subzone 11b

Definition - Interval from the last occurrence of very abundant (>20% of assemblage) *Z.noeliae* to the last occurrence of *Clepsilithus maculosus* (partial range subzone).

Author - Rutledge, this study.

Age - Latest Hauterivian (and very earliest Barremian?); equivalent to the *marginatus* ammonite Zone and the basal part of the *variabilis* Zone.

Records -
*Speeton: Beds C3(basal)-C2C(basal); 11 sa; *marginatus* Zone and basal *variabilis* Zone; c.3.5m thick; both lower and upper boundaries seen.
*Borehole 81/43: 28.10-22.90m (10 sa); both lower and upper boundaries seen.
*Core 7B: 5.00-4.50m (5 sa); upper boundary not cored.

Assemblage characteristics - As for the *C.maculosus* Zone, but *Z.noeliae* and *Micrantholithus* spp. are much depleted in abundance relative to the underlying subzone; both may be common/abundant, but they never dominate assemblages. *Rhagodiscus asper* and *Watznaueria* spp. are the dominant taxa. *Rhagodiscus pseudoangustus* is occasionally common within this interval.

Remarks - The LO of (rare) *Speetonia colligata* was recorded very close to the top of this interval in both Borehole 81/43 and Speeton - just below the base of the *variabilis* Zone at Speeton. Jakubowski (1987) recorded this event within the *variabilis* Zone of Speeton (unspecified horizon) - so it may lie slightly higher - but also below the LO of *"S.comptus"* (= *C.maculosus*). Jakubowski used the LO of *S.colligata* to mark the top of Zone NLK 14, but this species is rare towards the top of its range, and its LO its not thought to be a reliable datum at Boreal latitudes - both Crux (1989) and Mutterlose (1991) recorded this LO in considerably older strata (*staffi* and *gottschei* Zones, respectively).

Cretarhabdus inequalis Zone (BC 12)

Definition - Interval from the last occurrence of *Clepsilithus maculosus* to the first occurrence of *Nannoconus abundans* (interval zone).

Author - Crux, 1989, emend. this study.

Age - Early Barremian?; essentially equivalent to the *variabilis* ammonite Zone (= the upper part of the German *discofalcatus* ammonite Zone).

Records -

***Speeton**: Beds C2C(lower)-LB5E; 29 sa; c.2m thick; *variabilis* Zone; both lower and upper boundaries seen; whole interval highly condensed but sampled very closely (Crux, 1989, placed the upper boundary in the overlying *rarocinctum* Zone, but was limited by his sample density).

***Borehole 81/43**: 21.87-11.01m; 13 sa; both lower and upper boundaries seen; interval much expanded relative to Speeton.

Germany (Frielingen Pit): Beds 101-127 (interpolated from a range chart of Mutterlose, 1991a); *discofalcatus* Zone (upper?); neither upper nor lower boundaries are exposed.

Germany (Gott): Beds 50-?76 (interpolated from the range charts of Crux, 1989, and Mutterlose, 1991a); *discofalcatus* Zone (upper?) and basal *pugio* belemnite Zone?; upper boundary (taken from Crux) may be slightly too high (limited by Crux's sample density);

lower boundary unexposed, but Crux apparently mistakenly assigned the basal bed (50) to the *gottschei* Zone.

Assemblage characteristics - Dominated by *Watznaueria* spp., *R.asper* and *B.constans*. *C.inequalis*, *R.pseudoangustus* and *Tegumentum bergeni* var. *minor* are often common, and characteristic of this interval. *P.plethotretus* and *Z.scutula* occur throughout. *R.parallelus* is unusually abundant throughout much of this zone. A brief influx of *Diloma galiciense* in the upper part of this zone is correlatable between Speeton, Borehole 81/43 and (remarkably, considering the low number of samples obtained) Germany. Various Tethyan species of *Nannoconus* (*N.globulus*, *N.kamptneri*, *N.steinmannii*) are common within the paler horizons of this generally pale/dark rhythmically-bedded interval. *Nannoconus inornatus* becomes abundant in the upper part of this zone, just prior to the inception of *N.abundans* (these events are synchronous at Speeton due to condensation). *Assipetra terebrodentarius* appears towards the top of this zone; this FO is a reliable secondary datum (the relatively low reliability index at Speeton reflects the extremely close sampling of this interval).

Remarks - Two samples from the *discofalcatus* Zone of Frielingen Pit are assigned to the middle-upper part of this zone (= *variabilis* ammonite Zone = upper *discofalcatus* Zone), based on the absence of both *C.maculosus* and *A.terebrodentarius*, and the presence of *D.galiciense*. Mutterlose (1991a) sampled the Frielingen section more thoroughly, and did not record *C.maculosus*, so the lower part of the *discofalcatus* Zone is likely unexposed at this locality. The FO of *A.terebrodentarius* within this Zone is a useful event - this is synchronous in the Speeton section and Borehole 81/43, and probably also in Tethys (Bergen, 1994). This species has probably been included with *Assipetra infracretacea* by previous Boreal workers - thus it is not yet documented from Germany.

Nannoconus abundans Zone (BC 13)

Definition - Interval from the first occurrence of *Nannoconus abundans* to the first occurrence of *Nannoconus borealis* (?or the last occurrence of *Rhagodiscus pseudoangustus*) (partial range zone).

Author - Crux, 1989, emend. this study.

Age - Early Barremian; essentially equivalent to the *rarocinctum* ammonite Zone.

Records -

***Speeton:** Beds LB5D-LB3A(lower); 14 sa; c.10m thick; *rarocinctum* Zone (+ basal *fissicostatum* Zone?).
***Borehole 81/43:** 11.01-6.12m; 8 sa; upper boundary not cored.
Germany: Mutterlose (1991a) recorded the FO of (albeit very rare and sporadically occurring) *N.borealis* in the *brunsvicensis* belemnite Zone, well above the FO of *N.abundans* and only slightly above the LO of *R.pseudoangustus* (*Aulacoteuthis* belemnite Zone) recorded by Crux (1989).
?Danish Central Trough: Thomsen (1987) recorded the FO of (occasionally common) *N.borealis* above the FO of common (presumably true - see remarks) *N.abundans.*
?Moray Firth: Jakubowski (1987) indicated the FO of *N.borealis* above that of *N.abundans* (and above the LO of *S.colligata*) on his schematic range chart.

Assemblage characteristics - *N.inornatus* is often abundant, and is the dominant nannoconid within this interval, but fully-developed *N.abundans* is also conspicuous. *Rhagodiscus pseudoangustus* is a common and conspicuous element within this interval, and has its LO towards the top of the zone. Small forms of *Crucibiscutum* (=*C.salebrosum/pinnatus?*) are last recorded within this interval, but are rare and inconspicuous. *A.infracretacea* and *A.terebrodentarius* are common/abundant throughout; the latter species is especially characteristic of the interval. Small forms of *Tegumentum bergeni* (var. *minor*) seem virtually restricted to this and the underlying zone. As in the underlying zone, *R.parallelus* is unusually abundant within this interval. *C.margerelii* becomes abundant in the upper part of this interval, signalling the start of another major (middle Barremian) acme.

Remarks - Several previous authors (Taylor, 1982; Thomsen, 1987) have included short, flangeless nannoconids (here assigned to *N.inornatus*) in *N.abundans*, thus giving this species an anomalously early FO. Previous authors have also tended to overlook *N.borealis* - Crux (1989) did not record this species at all, despite extensive investigation of middle Barremian sections in Britain and Germany, and Mutterlose (1991a) recorded this species only very rarely. *N.borealis* does not occur very consistently (COR = 35% at Speeton), but is large, conspicuous and occasionally abundant, and its FO is probably a more reliable datum than the LO of *R.pseudoangustus* (which Crux used to define the top of this zone). The LO of *R.pseudoangustus* remains a useful datum, despite the sporadicity of this species' early record. Crux (1989) found the LO of *R.pseudoangustus* to be slightly higher at Speeton (at the base of the *fissicostatum* Zone), but recorded this event within the stratigraphically younger *Aulacoteuthis* belemnite Zone at Gott. However the correlation between the ammonite and belemnite zones may be imprecise (see Rawson & Mutterlose, 1991). Thus, it seems that these two nannofossil events (FO of *N.borealis* and LO of *R.pseudoangustus*) are sufficiently close to be complimentary.

Mutterlose (1991a) recorded an isolated (reworked?) occurrence of *R.pseudoangustus* in the considerably younger *brunsvicensis/germanica* Zone.

Forms apparently transitional between *N.abundans* and *N.borealis* (here assigned to *N.borealis* var. A) were observed to have a FO synchronous with that of typical, fully-formed *N.borealis* (var.B), but this interval was not very closely sampled. Closer sampling may reveal a temporal gradation between these forms. *N.borealis* var.A was recorded from the *Aulacoteuthis* Zone of Gott, which suggests that the FO of *N.borealis* and the LO of *R.pseudoangustus* (as recorded by Crux) are very close in Germany. *N.borealis* var.A has also been recorded from the Barents Sea (Jacob Verdenius, *pers. comm.*). *R.pseudoangustus* certainly ranged into the Barents Sea, but the exact timing of its LO in this region is not yet certain. Jakubowski (1987) used the LO of *C.salebrosum* (= *C.pinnatus?*), which occurs within this interval, to mark the top of his Zone NLK 13, but this species is considered too rare and inconspicuous in the upper part of its range to be of any use.

Nannoconus borealis Zone (BC 14)

Definition - Interval from the first occurrence of *Nannoconus borealis* (or the last occurrence of *Rhagodiscus pseudoangustus*) to the first consistent occurrence of common/abundant *Zeugrhabdotus scutula* (partial range zone).

Author - ?Crux, 1989 (= *Cretarhabdus conicus* Zone) emend. this study.

Age - Early Barremian; essentially equivalent to the *fissicostatum* ammonite Zone (and the basal part of the *elegans* Zone), or the *Aulacoteuthis* spp. belemnite Zone.

Records -
*Speeton: Beds LB3A(mid)-LB1A(lower); 34 sa; c.15m thick; *fissicostatum* Zone to *elegans* Zone.
*Germany (Gott): Beds ?100-102 (after Crux, 1989); *Aulacoteuthis* spp. Zone; my own samples from the "Hauptblätterton" unit lack *R.pseudoangustus*, *Z.scutula* and *N.pseudoseptentrionalis*, but yield *N.borealis* var.A, substantiating the assignment of this interval to Zone BC 13.

Assemblage characteristics - Assemblages are often of low diversity and dominated by a few conspicuous elements - *R.asper*, *C.margerelii*, *Micrantholithus* spp. and *Nannoconus* spp.. Both *N.inornatus* and *N.abundans* are common/abundant throughout much of this interval; the latter, flanged species is generally dominant. *N.borealis* is more sporadic in its occurrence but very conspicuous and occasionally abundant. In addition, a

variety of other aberrant nannoconids are present. *Axopodorhabdus dietzmannii* and *Tubodiscus parvus* are unusually abundant in this interval. *Sollasites horticus* is often common/abundant. Overall nannofossil abundance is generally relatively low. A considerable number of coccolith species disappear within this zone, but these disappearances may be environmentally induced and not representative of true extinctions (see Remarks).

Remarks - All these characters suggest stressful environmental conditions. This zone corresponds approximately with an interval of organic-rich clay deposition (Blätterton facies) which represents a middle Barremian kenoxic event (Rawson & Mutterlose, 1983). This interval is represented in the central North Sea by the Munk Marl Bed (Thomsen, 1987). A number of species seem to have been strongly averse to these conditions - *R.pseudoangustus*, *A.terebrodentarius*, *H.ellipticus*, and *T.jurapelagicus* disappear at or near the base of the zone. Several of these highest occurrences may represent true extinction events - only *A.terebrodentarius* is known to reappear after cessation of Blätterton deposition. *Diloma primitiva* and *Cretarhabdus radiatus* have their HOs rather higher in this interval; these are likely true extinction events. *C.rothii* is extremely rare within this zone, but is known to reappear later in the Barremian (see discussion later). Nannoconids undergo considerable diversification during this interval, but their are no known evolutionary originations of coccoliths.

Zeugrhabdotus scutula Zone (BC 15)

Definition - Interval during which *Zeugrhabdotus scutula* is consistently common/abundant (2-15% of assemblages), in the presence of other characteristic Barremian forms (notably *N.abundans* and *N.borealis*).

Author - Rutledge, this study.

Age - Mid-Barremian; equivalent to the *elegans* to ?*innexum* ammonite Zones.

Records -

***Speeton**: Beds LB1A(mid)-Cement Bed 47; 6 samples; at least 4m thick; *elegans-denckmanni* Zones; upper boundary unexposed, but must lie within the Cement Beds (*denckmanni/innexum* Zones) since *Z.scutula* is much reduced in abundance in a short, sampled section of the Upper Cement Beds (?*stolleyi* Zone).

Germany (Gott): Beds 102-131 (interpolated from a range chart of Crux, 1989); upper *Aulacoteuthis* spp. Zone to lower *germanica* Zone.

Germany (Hoheneggelsen M 14 section): Beds 81-?100 (interpolated from a range chart of Mutterlose, 1991a); *brunsvicensis* to *germanica* Zones.

Danish Central Trough (Well E 1): 8219-8211 feet (interpolated from a range chart of Thomsen, 1987); *"Z.sisyphus"* (= *Z.scutula*) is common/abundant in three consecutive samples from above the Munk Marl Bed, i.e. post-*fissicostatum* ammonite Zone, which also yield *N.abundans* and *N.borealis.*

Assemblage characteristics - The remarkable feature of this interval is the consistently high relative abundance of *Z.scutula. Nannoconus pseudoseptentrionalis* is also characteristic of this zone, at least in its lower part. *Acaenolithus?* sp.1 first appears in the middle of this interval. *N.abundans* is often common, and *N.borealis* generally rare (but Perch-Nielsen, 1979, recorded this species commonly in the Cement Beds of Speeton).

Remarks - Abundance estimates vary among authors. Thus, Mutterlose (1991a) indicated that *"Z.sisyphus"* (= *Z.scutula*) was relatively uncommon (<5%) through much of this interval in the Gott section. My own observations on this part of the Gott section (on four samples from the *?germanica* Zone) confirm abundances of 2-5%, but these are still consistent with Crux's (and my own) definition of common/abundant. Such a level of abundance ensures that, in a slide of average thickness, a specimen is located in every one or two fields of view and very many specimens are seen during a routine traverse. This species often attains much greater levels of abundance within this Zone - relative abundances of >10% were recorded in the Speeton section, and Mutterlose recorded similar figures in the Hoheneggelsen section. *Z.scutula* is a large and conspicuous species, and this sustained acme is easily recognised. Only very rarely does this species attain these levels of abundance outside this interval.

Z.scutula was not recorded from the Barents Sea, so this zone is probably limited in its geographical applicability. However this species certainly ranged as far north as mid-Norway (Core 7B), and its mid-Barremian acme is likely recognisable throughout the North Sea.

Crux (1989) used the re-entry of *T.septentrionalis* to mark the base of his *Z.sisyphus* Zone, but he had mistakenly identified a small nannoconid, here assigned to *N.pseudoseptentrionalis.* The FO of this form is a useful secondary datum to mark the base of BC 15. *N.pseudoseptentrionalis* seems restricted to lower part of this zone - Crux recorded the LO of *"T.septentrionalis"* in the *brunsvicensis* Zone at Gott, and this form was not recorded in this study's *?germanica* Zone samples.

Both Crux (1989) and Mutterlose (1991a) used the FO of *"Vagalapilla matalosa"* to mark the top of their *Z.sisyphus* Zones, and the base of an overlying *V.matalosa* Zone, but neither author was aware of the existence of very similar forms much earlier in the

Barremian. The taxonomic position of this form remains uncertain, but it is assigned to *Acaenolithus?* sp.1 in this study. It does seem distinct from the earlier, similar forms (tentatively assigned to *Diloma?* sp.), but it is doubtful whether these could be reliably differentiated. Nevertheless, the first consistent occurrence of *Acaenolithus?* sp. remains a useful event - I recorded this form consistently in the *?germanica* Zone, and Crux recorded the FO of this form in the *brunsvicensis* Zone of Gott, in the middle of the *Z.scutula* acme interval. Mutterlose recorded the FO of *"V.matalosa"* higher, in the *germanica* Zone, above the *Z.scutula* acme. Thus BC 14 overlaps the *V.matalosa* Zone of Crux, but not the *V.matalosa* Zone of Mutterlose.

The LO of *Apertasphaera jakubowskii* may lie within this interval - the highest recorded occurrences in both Crux (1989) and this study are in this zone, although Mutterlose (1991) recorded it higher. Jakubowski (1987) found the LO of this species (as *"Diazomatolithus lehmanii"*) to be a useful Lower Barremian datum in the Dutch Sector of the North Sea.

Acaenolithus? sp. Zone (BC 16)

Definition - Interval from the last consistent occurrence of common/abundant (2-15% of assemblage) *Zeugrhabdotus scutula* to the last occurrence of *Nannoconus borealis* (partial range zone).

Author - Rutledge, this study.

Age - Late Barremian; equivalent to the *?innexum* to *?bidentatum* ammonite Zones.

Records -

Germany (Hoheneggelsen M 14 section): Mutterlose (1991) recorded the LO of *N.borealis* above the LO of common/abundant *Z.sisyphus* (= *Z.scutula*), within the *germanica* Zone.

***Speeton ?:** the LO of common/abundant *Z.scutula* is within the Cement Beds (= pre *?stolleyi* Zone), but *N.borealis* var.A was recorded in the stratigraphically younger, lower part the Heslerton Borehole, above the LO of common/abundant *Z.scutula.*

?Moray Firth: Jakubowski (1987) recorded the LO of *N.borealis* above the LO of *C.rothii*, using these two datums to define his *N.borealis* Zone. The highest (rare) occurrence of *C.rothii* observed in this study is in the Lower Barremian *fissicostatum* Zone of Speeton, but my coverage of the Upper Barremian is incomplete; Mutterlose (1991a) recorded this very distinctive species as high as *N.borealis* in the Hoheneggelsen section. If Jakubowski was correct in his sequencing of these events (and wrong in his

mid-Barremian age assignment - he utilised a now out-dated 3-fold division of the Barremian) then *N.borealis* must range considerably above the top of the *Z.scutula* acme.
?Danish Central Trough (Wells E 1 and 1-1): Thomsen (1987) recorded *N.borealis* fairly commonly up to the (apparently truncated) top of the Tuxen Formation, well above the Munk Marl Bed (= *fissicostatum* Zone), and throughout the duration of a *"Z.sisyphus"* acme (= 3 consecutive samples) in Well E1. His lack of records of *N.borealis* above this acme interval may be explained by a stratigraphical break between the Tuxen and the overlying Sola Formation. Like Jakubowski (1987), he recorded the LO of *N.borealis* well above that of *C.rothii* (which he placed shortly above the Munk Marl Bed, in a position consistent with Mutterlose's LO of this species).

Assemblage characteristics - These can only be inferred, but must include *N.abundans*, *N.borealis*, and *Acaenolithus?* sp.1 (= the "V.matalosa" of previous authors).

Remarks - Evidence for the existence of this zone is admittedly scant, but then so is the evidence for the various ammonite zones proposed for this interval. This is due mainly to persistent non-exposure of this interval at Speeton, and to the rarity of ammonites in the German sections. Due to the lack of sample material from this interval, I have tried to recalibrate the published onshore and offshore evidence; if this has succeeded then the LO of *C.rothii* must lie within this zone, but this species has a discontinuous range and this is probably not a reliable datum. *N.borealis* also has a rather discontinuous range, but would seem to be quite consistently present in the Upper Barremian. Further investigation of offshore sections (and/or fortuitous exposures at Speeton) may enable this zone to be proven.

Biscutum constans Zone (BC 17)

Definition - Interval from the last occurrence of *Nannoconus borealis* to the first occurrence of *Rhagodiscus angustus parvus* and/or the re-entry of common *Watznaueria britannica* (interval zone).

Author - Rutledge, this study.

Age - Latest Barremian; equivalent to the *bidentatum* ammonite Zone?

Records -
***Heslerton Borehole 2:** 27.93m-c.18m; 23 sa; *N.borealis* var.A (but not var.B) occurs near the base of this section.

Danish Central Trough: Thomsen (1987) recorded a clear separation between these nannofossil datums in a cored section of Well E-1 (lower Sola Formation); this zone is, however, missing in Wells ADDA-2 and 1-1, due to a disconformity at the base of the Sola Formation (in these two wells *R.angustus* and/or common *W.britannica* appear at the very base of the Sola Formation, immediately above the LO of *N.borealis*).
?Germany: The latest Barremian clays examined in both Mutterlose (1991a) and this study are barren of nannofossils, but compilation of Mutterlose's data indicates a separation between the ranges of the aforementioned marker species. Mutterlose (1991a) recorded consistently abundant (>20%) *B.constans* within the, albeit impoverished assemblages from the upper *germanica* and *depressa* belemnite Zones of Gott; this feature is also observed throughout the lower part of the Heslerton Borehole.

Assemblage characteristics - Dominated by *Biscutum constans*, with occasional *N.abundans*, and *Acaenolithus?* spp.. *Acaenolithus?* spp. decrease in size during this interval, from c.7μm (sp.1) to 3-4μm (sp.2) in length. Regularly-formed *T.octiformis* may have its LO at about the top of this interval.

Remarks - The FO of *R.angustus* has previously been used to mark the base of the Upper Aptian (e.g. Thierstein, 1973; Perch-Nielsen, 1979; Taylor, 1982; Jakubowski, 1987), but these authors had insufficient Lower Aptian material, or were unable to place FODs reliably due to the limitations of cutting samples (Jakubowski, 1987). Thomsen (1987) and Mutterlose (1991a) observed small forms of *R.angustus* commonly in the Lower Aptian of the North Sea area, and such forms are observed in the basal Aptian (Skegness Clay and basal Atherfield Clay) in this study. These forms are obviously transitional with larger, more elongate forms of *R.angustus* (= the typical *R.angustus* of previous authors), and are here assigned to *R.angustus* subsp. *parvus*. The FO of *R.angustus parvus* coincides approximately with a dramatic influx of *W.britannica* (a predominantly Jurassic species that is very rare within the Neocomian).

Watznaueria britannica Zone (BC 18)

Definition - Interval from the first occurrence of *Rhagodiscus angustus parvus* (or the re-entry of common *Watznaueria britannica*) to the first occurrence of *Farhania varolii* (partial range zone).

Author - Mutterlose, 1991 (= *Chiastozygus litterarius* Zone) emend. this study.

Age - Early Aptian; equivalent to the *fissicostatus* and the lower part of the *forbesi* ammonite Zones.

Records -

Germany (Hoheneggelsen KB 9 Well): Mutterlose (1991a) recorded the FO of *F.varolii* (B 7/10 sa) in the "Fischschiefer", above the FOs of *R.angustus* and common *W.britannica*

Danish Central Trough (Wells E1 and ADDA-2): Thomsen (1987) recorded the FO of *F.varolii* (B 10/10 sa in Well E1) shortly above the FOs of *R.angustus* and common *W.britannica* in cored sections from these two wells. In both instances, the FO of *F.varolii* is around the top of a finely-laminated black shale unit in the lower part of the Sola Formation, which is lithologically comparable to the "Fischschiefer" of Northern Germany and Helgoland. Furthermore, Thomsen examined material from a condensed (1m thick) outcrop of the "Fischschiefer" in Helgoland (dated as upper *forbesi* Zone), recording *R.angustus*, *F.varolii* and common *W.britannica*.

*Heslerton Borehole 2: c.18m-12.13m (16 sa); *F.varolii* is quite common on its first appearance, but its low COR (B 2/7 sa) in the overlying (short) Aptian section may be explained by a stratigraphical break at c.12m.

*Skegness Borehole: Skegness Clay (lower *fissicostatus* Zone); upper boundary not seen (truncated); the FO of *R.angustus parvus* was recorded within this basal Aptian deposit, suggesting that this datum is a good approximation for the base of the Aptian. *W.britannica* is rare/absent in this horizon, suggesting that the *W.britannica* influx began slightly later.

*Atherfield Clay (Isle of Wight): Perna Beds and lower Chale Clay (upper *fissicostatus* to lower *forbesi* Zones); upper boundary not seen (barren section); the *W.britannica* influx is especially evident in the Perna Beds.

Assemblage characteristics - *R.angustus parvus* increases in abundance throughout this zone, becoming common/abundant. *W.britannica* is common/abundant throughout much of the interval. Small forms of *Acaenolithus?* (3-4μm long) are often common. *F.oblongus* and *H.irregularis* first appear within this zone (post *fissicostatus* Zone); the FO of the former species is a useful datum, but *H.irregularis* has a much less consistent range. The LO of *N.abundans* was recorded in this part of the Heslerton Borehole.

Remarks - The upper boundary of this zone is approximately equivalent to the top of the "Fischschiefer", a thin but distinctive horizon that is widespread throughout the North Sea. This organic-rich deposit is apparently slightly diachronous; Thomsen (1987) and Mutterlose (1991a) recorded *F.varolii* and *F.oblongus* within their thin, onshore "Fischschiefer" units, but these species first appear at the top of, or shortly above the (thicker) equivalent lithological units in the Heslerton Borehole and Well E1. Thomsen's Helgoland "Fischschiefer" was ammonite-dated as upper *forbesi* Zone but, applying the limited nannofloral evidence from the Isle of Wight, it seems that black shale deposition began earlier (*fissicostatus* Zone) in other areas. The base of the "Fischschiefer" (= base

of the Sola Formation in the Danish Sector of the North Sea) is clearly disconformable in Wells ADDA-2 (Thomsen, 1987) and Hoheneggelsen KB 9 (Mutterlose, 1991); this must reflect a sea-level event during the *forbesi* Zone. *N.abundans* was recorded in 3/3 samples immediately above the "Fischschiefer" in the Heslerton Borehole; there are no other obvious signs of reworking (other than, perhaps, fairly common *C.margerelii*) in these samples. This casts doubt on the use of this species' LO as a latest Barremian datum (Taylor, 1982; Jakubowski, 1987; Mutterlose, 1991a). In any case, *N.abundans* is quite rare in its upper range, and its LO is not a reliable datum.

Farhania varolii Zone (BC 19)

Definition - Interval from the first occurrence of *Farhania varolii* to the first occurrence of *Lithraphidites moray-firthensis* (partial range zone).

Author - Rutledge, this study.

Age - Early Aptian; equivalent to the upper *forbesi* to ?lower *deshayesi* ammonite Zones.

Records -

***Heslerton Borehole 2:** 12.13m-10.49m (6 sa); condensed (there is a nannofloral turnover above a sharp lithological contact at c.12m).

Danish Central Trough (Well E1): Thomsen (1987) recorded the FO of *L.moray-firthensis* shortly above that of *F.varolii* (B 10/10 sa), within the Sola Formation.

"Fischschiefer" (Helgoland): Thomsen (1987) recorded *F.varolii*, but not *L.moray-firthensis*, in this condensed deposit (ammonite-dated as upper *forbesi* Zone).

Germany (Hoheneggelsen KB 9 Well): Mutterlose (1991a) recorded the FO of *F.varolii* (B 7/10 sa) in the "Fischschiefer"; upper boundary not seen.

Assemblage characteristics - Very abundant *B.constans* (c.40% in the Heslerton Borehole, but rather less abundant in Germany), with common *R.angustus parvus*, *F.varolii*, and *F.oblongus*. *W.britannica* declines in abundance to its normal, background level (rare) early in this zone. Major influxes of *R.parvidentatum* and *Z.xenotus* occur in the Heslerton Borehole. This first common occurrence of *R.parvidentatum* may represent the evolutionary origination of this very small species - Thomsen (1987) recorded the FO of (SEM confirmed) *R.parvidentatum* at a similar level. *Lithraphidites ?pseudoquadratus*, the likely precursor of *L.moray-firthensis*, may be fairly common. The FO of *Rhagodiscus fenestratus* was recorded in this interval.

Remarks - *F.varolii* is a distinctive and dissolution-resistant species, with a wide geographical distribution. Varol (1992) recorded this species in Angola, India and

Indonesia. It has also been recorded from the Indian Ocean (*pers. obs.*). Previous records of *"Lithastrinus septentrionalis"* from low-latitude Aptian sections (Thierstein, 1973; Roth, 1983) almost certainly belong to this species. Early, rare records of *"Eprolithus apertior"* from this interval (Thomsen, 1987; Mutterlose, 1991a) were probably overgrown, or aberrant specimens of *F.varolii*.

Lithraphidites moray-firthensis Zone (BC 20)

Definition - Interval from the first occurrence to the last consistent occurrence of *Lithraphidites moray-firthensis* (?total range zone).

Author - Jakubowski, 1987, emend. this study.

Age - Early Aptian; probably roughly equivalent to the *deshayesi* ammonite Zone.

Records -

***Heslerton Borehole 2:** 10.49m-10.29m (2 sa); *L.moray-firthensis* is common in one reasonably preserved sample; upper boundary not seen (barren and condensed section).

Danish Central Trough: Thomsen (1987) recorded common *L.moray-firthensis* in the uppermost part of Well E1 (upper boundary not cored).

Moray Firth: Jakubowski (1987) used the LO of common *L.moray-firthensis* as an intra-Lower Aptian datum, but could not place accurately the FO of this species due to the limitations of cutting samples.

Assemblage characteristics - Common *L.moray-firthensis*, with *F.varolii* and *R.parvidentatum*.

Remarks - Jakubowski (1987) recorded *L.moray-firthensis* rarely in the Upper Aptian, and hence used the last common occurrence of the species as a datum. However, this species has never been described in any dated mid-late Aptian outcrop material, and is probably restricted to the Lower Aptian (*deshayesi* Zone?). Jakubowski's later records may have been reworked or misdated. The FO of this species can now be constrained to the intra-Lower Aptian, above the FO of *F.varolii*. Jakubowski noted that his *L.moray-firthensis* Zone (NLK 9) was difficult to detect in areas of the North Sea due to condensation of the Lower Aptian; this is borne out in the present study.

Rhagodiscus asper Zone (BC 21)

Definition - Interval from the last consistent occurrence of *Lithraphidites moray-firthensis* to the last occurrence of *Farhania varolii* (partial range zone).

Author - Jakubowski, 1987, emend. this study.

Age - "Middle" to Late Aptian; equivalent to the *?bowerbanki* to *jacobi* ammonite Zones.

Records -
***Skegness Borehole:** Sutterby Marl (undifferentiated Late Aptian); *pars.*.
***Germany (Gott marls):** *nutfieldiensis* Zone; *pars.*.
Germany (Arpke 2 section): interpolated from Mutterlose, 1991a; *jacobi* Zone; upper boundary recognised.
Germany (Rethmar section): interpolated from Mutterlose, 1991a;"*ewaldi*-Mergel" (middle Aptian); *pars.*.
Helgoland: interpolated from Mutterlose, 1991a; "gelbe *ewaldi*-Kriede"; *bowerbanki* Zone & uppermost *deshayesi* Zone?; *pars.*.
Helgoland: interpolated from Thomsen, 1987; "rote *ewaldi*-Kriede"; *martinoides* Zone; *pars.*.
Moray Firth : equivalent to Jakubowski's (1987) Zones NLK 7-8.

Assemblage characteristics - *R.asper* is very abundant (c.20-50% of assemblages) throughout much of this interval, but undergoes a terminal decline in abundance towards the top of the zone. *R.parvidentatum* is common/abundant, particularly towards the top of the zone. *Nannoconus* spp. (especially *N.truitti* and *N.quadriangulus*) may be common. *Braarudosphaera* spp. (especially *B.africana*), *R.orbiculatus/planus* and *E.floralis* are also characteristic of this interval; these species have their FOs near the base of this zone (possibly in the underlying zone). *Crucibiscutum* sp. cf. *C.salebrosum* may be common towards the top of the zone. *Micrantholithus* spp. becomes rare, and may disappear entirely towards the top of this interval. *F.varolii* can be rare, but is consistently present throughout the zone.

Remarks - Jakubowski (1987) subdivided this interval using the LO of abundant *R.asper* but utilised the LO of common/abundant *R.asper*, above the LO of *F.varolii*, to define another zonal boundary. Jeremiah (*in press*) utilises the last consistent occurrence of a "high relative abundance" of *R.asper*, also recognised in offshore sections, to define a ?latest Aptian or Early Albian zonal boundary. However neither of these authors use well-defined abundance categories, so the placement of this datum relative to the LO of *F.varolii* remains uncertain. The presently available onshore data suggests that there is a major decline in the abundance of *R.asper* (from >20% to c.5%) within the *nutfieldiensis* Zone, prior to the LO of *F.varolii* (*jacobi* Zone). Jakubowski (1987) further subdivided

this interval using the FOs of *R.angustus* and *"E.apertior"* (= 9 rayed forms of *Radiolithus* and *Eprolithus*); the former species has been shown to have originated in the earliest Aptian, while the exact level of origination of the latter lineage remains uncertain. There remains great potential for subdividing this long interval, since many species originate in the mid-late Aptian. Further subdivision must await the availability of offshore core material; unfavourable facies and incomplete sections onshore make it very difficult to piece together the patchy outcrop data.

Repagulum parvidentatum Zone (BC 22)

Definition - Interval from the last occurrence of *Farhania varolii* to the first occurrence of *Prediscosphaera columnata* (interval zone).

Author - Jakubowski, 1987, emend. this study.

Age - Latest Aptian to Early Albian; equivalent to the upper *jacobi* ammonite Zone and an uncertain portion of the Lower Albian.

Records -
Moray Firth: equivalent to NLK 6 and NLK 5B of Jakubowski, 1987.
Germany (Arpke 2 section): interpolated from Mutterlose, 1991a; *jacobi* Zone; *pars.* (base seen).
Germany (Vöhrum): interpolated from Mutterlose, 1991a; *jacobi* Zone; *pars.*.
Germany (Vöhrum): interpolated from Jeremiah, *in press*; earliest Albian; *pars.*.
Speeton: interpolated from Jeremiah, *in press*; Bed A5 (*ewaldi* Marl); *pars.*.
U.K. Central North Sea: interpolated from Jeremiah, *in press*; lower Rødby Fm. and upper Sola Fm.; *pars.*.
***Heslerton Borehole 2 ?**: condensed out/barren, but the FO of *P.columnata* is identified in the Early Albian (below the LO of *A.viriosus*).

Assemblage characteristics - Common/abundant *R.parvidentatum* (="Coccolith" of Mutterlose, 1991, in the Vöhrum section?). *R.asper* is much reduced in abundance relative to the underlying zone. *A.viriosus* and *S.primitivum* first appear within this interval; the former species is almost restricted to this interval (having its LO shortly above the FO of *P.columnata*), while the latter is particularly abundant, upon its appearance. The first consistent occurrence of *R.splendens* lies within this interval; earlier, generally rare, records of this species were probably aberrant specimens of *R.asper/fenestratus*.

Remarks - As in the underlying zone, a number of species originate in or around this interval, but their FOs cannot be precisely constrained. The FO of *P.columnata* provides a convenient, and widely recognised datum (e.g. Thierstein, 1973) for the definition of an upper boundary. Further investigation of dated outcrop sections should enable precise definition of the Aptian/Albian boundary. This zone overlaps part of Jeremiah's NAL 1.

3.5 - INTER-REGIONAL CORRELATION

The standard Lower Cretaceous stages are defined in south-east France, by means of ammonite biostratigraphy, and correlation of the Neocomian stages with more northerly, Boreal areas has always been problematical. Ammonite provincialism has necessitated the development of very different zonations in Boreal and Tethyan areas, and was so strong in the Berriasian and Barremian that inter-regional correlation has been virtually impossible. Thus a different stage name - the Ryazanian - is used, rather loosely, in place of the Berriasian at Boreal latitudes. There was some mixing of ammonite faunas during Valanginian and Hauterivian times, enabling Boreal and Tethyan schemes to be tied together using immigration horizons (Fig. 3.13, modified after Kemper *et al.*, 1981). Detailed correlation of Valanginian sections has been achieved (Kemper *et al.*, 1981), but the Hauterivian of Boreal and Tethyan areas is less well integrated.

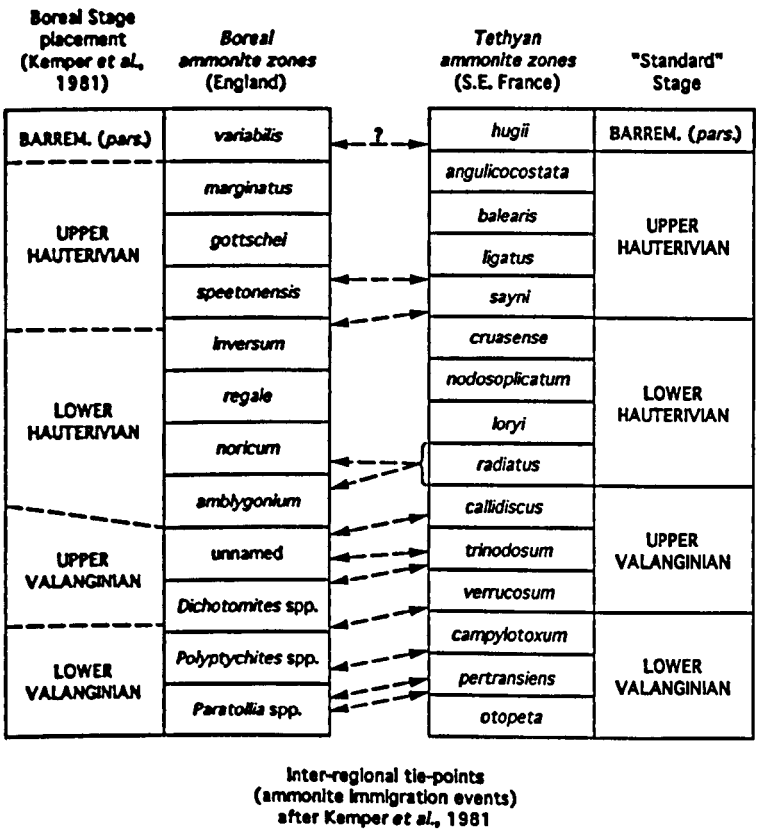


Fig. 3.13 - Correlation of Boreal and Tethyan ammonite zonal schemes (after Kemper *et al.*, 1981). The Hauterivian-Barremian ammonite zonal scheme for the Tethyan region is modified in accordance with Hoedemaeker & Bulot (1990) and Hoedemaeker & Company (1993) as communicated by Bulot *in* Bergen (1994).

Nannofossil zonation schemes applied to the Neocomian of Boreal and Tethyan areas have seemed virtually irreconcilable, utilising entirely different suites of marker species. Bralower (1991) attempted to integrate Boreal and Tethyan nannofossil events by paying particular attention to the ranges of (rare) Tethyan marker species in a key Boreal section (Borehole 81/43). Based on the ranges of three predominantly Tethyan taxa (*T.verenae*, *C.cuvillieri* and *S.colligata*), that were supposedly well-constrained in Tethyan sections, Bralower proposed that both the Valanginian-Hauterivian and Hauterivian-Barremian boundaries may have been misplaced very considerably at Speeton, and thus throughout northern Europe. These proposals were contrary to a considerable volume of ammonite evidence (e.g. Kemper *et al.*, 1981). However, the basic premises on which Bralower's correlations were made are shown to be erroneous:

(1) LOD of *Tubodiscus verenae* - Thierstein (1973) found this species to be restricted to the Valanginian of S.E. France, and Roth (1978, 1973) subsequently used its LOD as an Upper Valanginian zonal marker. Thus, Bralower (1991) believed *T.verenae* to be an essentially Valanginian species, even though Applegate & Bergen (1988) had recorded it rarely up to the Upper Hauterivian of ODP Site 638 (eastern North Atlantic). Subsequent work has confirmed that *T.verenae* did linger on into the Late Hauterivian in both Tethys (Bergen, 1994, records the LO in the *sayni* Zone of S.E. France) and the North Sea (I recorded *T.verenae* 15m higher than Bralower in Borehole 81/43, is strata of indisputable Late Hauterivian age).

(2) LOD of *Speetonia colligata* - All published data from the Tethyan stratotypes (Thierstein, 1973, 1976; Bergen, 1994) and deep-sea (Applegate & Bergen, 1988; Bergen, 1994) place this event very clearly in the Upper Hauterivian, yet Bralower (1991) assigned this datum an Early Barremian age and used the mid-point between it and the LOD of *C.cuvillieri* (an established Upper Hauterivian datum) to infer a Hauterivian-Barremian boundary. This is a flagrant misuse of these nannofossil datums.

While it is clear that some of the most easily utilised markers in each realm have restricted palaeogeographical distributions, improved documentation of sections in Tethys (Applegate & Bergen, 1988; Bergen, 1994) and the Boreal area (this study) has revealed the potential for direct inter-regional correlation. Following Thierstein (1971, 1973), Tethyan nannofossil workers have relied heavily on two species, *Calcicalathina oblongata* and *Lithraphidites bollii*, to subdivide the Neocomian. These most stenothermal of species only very rarely reached Boreal latitudes; they are also relatively long-ranging, so brief influxes into Boreal areas are of little use in correlation. A number of other, recently utilised Tethyan markers also appear to have been very temperature sensitive (e.g. *Cyclagelosphaera deflandrei*, *Rhagodiscus dekaenelii*, *Helenea quadrata*, *Zeugrhabdotus erectus*), and their LODs are likely to be strongly diachronous on an inter-regional scale.

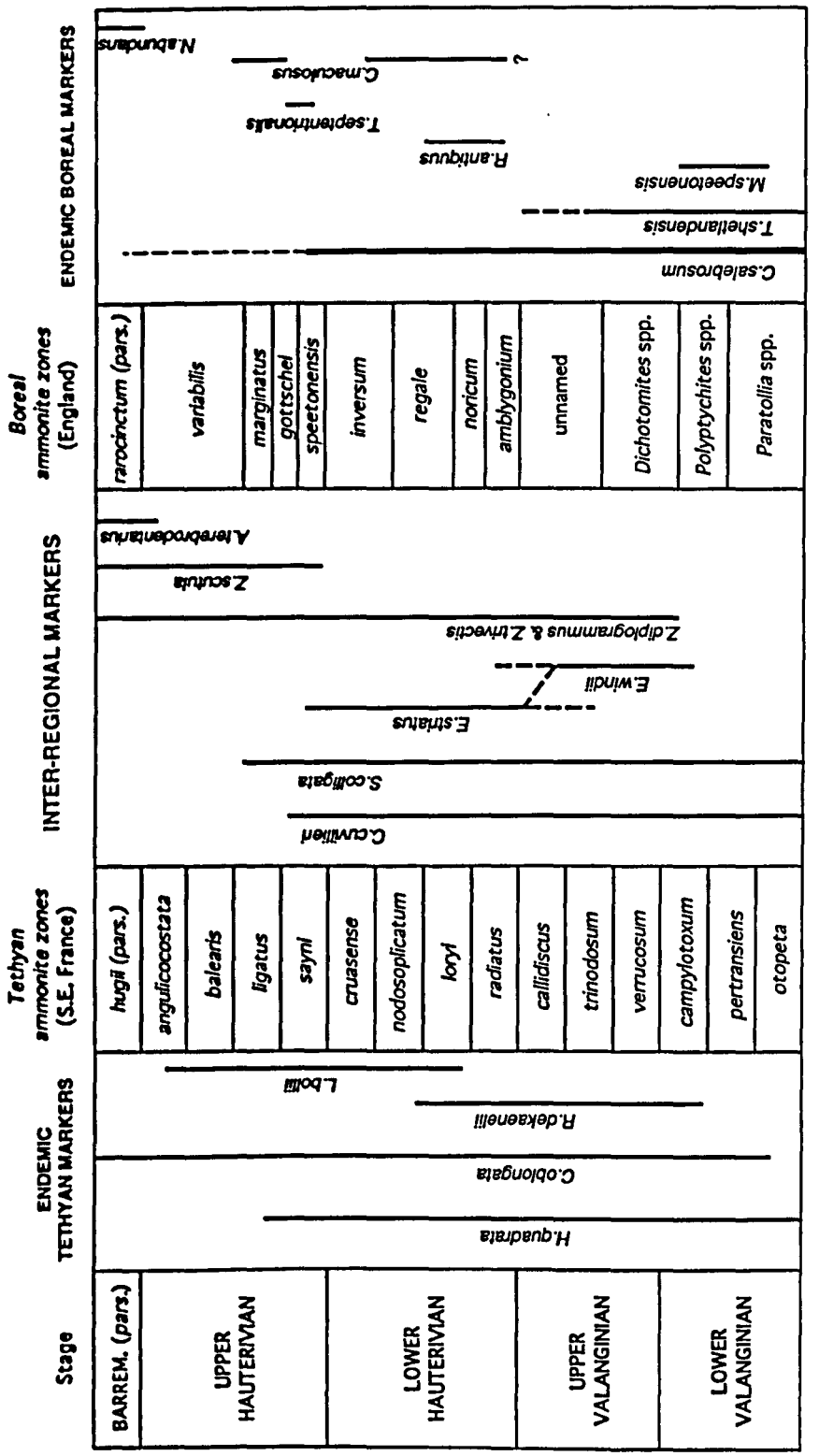


Fig. 3.14 - Ranges of primary Boreal, Tethyan and inter-regional nannofossil marker species (Tethyan ranges from Bergen, 1994). Boreal ammonite zones are calibrated against Tethyan zones using the available nannofossil data. The ranges of *E.striatus* and *Z.scutula* are shown overlapping, as observed in this study (Bergen, 1994, recorded a separation between the ranges of these species, possibly due to condensation of his Upper Hauterivian sections).

Fortunately some of the most useful Boreal markers are very short-ranging (e.g. *M.speetonensis*, *R.antiquus*, *T.septentrionalis*), and even limited occurrences in Tethyan sections are likely to be useful in inter-regional correlation. Bergen (1994) has recently documented two such species (*M.speetonensis* and *R.antiquus*), previously thought to be restricted to the Boreal area, in Tethyan sections. Several other key Boreal markers, undocumented by Bergen, are known to be present in Tethyan sections. *T.shetlandensis* has been observed commonly, with *M.speetonensis*, in a Lower Valanginian sample from Angles, S.E. France (*pers. obs.*). Additionally, *T.septentrionalis* is known to occur in the western North Atlantic (Roth, 1983), California (Bralower, 1989), Indonesia (Varol, 1991), and S.E. France (Silvia Gardin, *pers. comm.*). This species is an extremely useful marker, with a total range of comparable duration to an ammonite zone. Condensation of Bergen's Upper Hauterivian sections might account for his lack of records of *T.septentrionalis*; this would also explain his anomalous sequencing of the FOD of *Z.scutula* and the LOD of *E.striatus*, relative to the sequence of events observed in the (expanded?) Upper Hauterivian of this study.

Taxonomic improvements, with the application of more restricted species concepts, have shown that many other species are common to both realms. Thus *E.windii*, *E.striatus*, *Z.diplogrammus*, *Z.trivectis*, *Z.scutula* and *A.terebrodentarius* are potentially useful inter-regional markers; previous Boreal workers have had broader concepts of these species, or overlooked them entirely. Improved documentation of the ranges of *C.cuvillieri* and *S.colligata*, which have previously been used as markers in both Boreal and Tethyan areas, has provided further inter-regional datums (Fig. 3.15).

A preliminary nannofossil-based correlation of the Valanginian-Hauterivian of Boreal and Tethyan regions is presented in Fig. 3.15. This agrees remarkably well with traditional, ammonite-based correlations (compare with Fig. 3.13). The lack of Upper Valanginian sample material in this study limits the degree of correlation, but the nannofossil datums agree well with current positioning of the Lower/Upper Valanginian boundary in Boreal sections. Extreme condensation of Lower Hauterivian sections limits the degree of correlation in this interval, but there is certainly no evidence to suggest that the Valanginian/Hauterivian boundary has been misplaced in Boreal sections (as suggested by Bralower, 1991). Mid-Hauterivian nannofossil datums are in good agreement with current positioning of the Lower/Upper Hauterivian boundary in Boreal sections (high in the *inversum* Zone). Re-study of the (condensed?) Tethyan sections should reveal the presence of *T.septentrionalis* in this interval, and allow proper sequencing of the FOD of *Z.scutula* and the LOD of *E.striatus*.

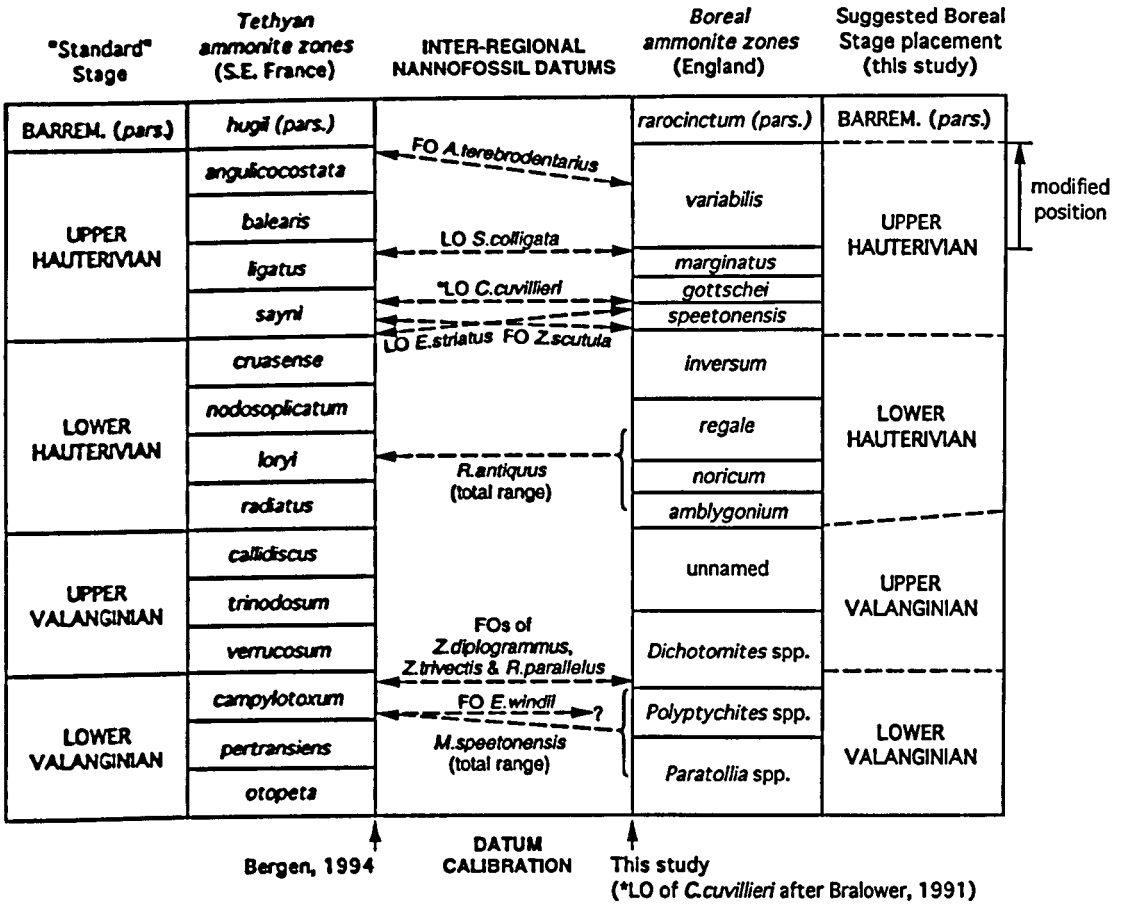


Fig. 3.15 - Preliminary nannofossil-based correlation of Boreal and Tethyan ammonite zonal schemes. Based on these nannofossil datums, it is proposed that the Hauterivian/Barremian boundary be raised in Boreal sections to the top of the *variabilis* ammonite Zone. FO = first occurrence; LO = last occurrence.

The only point of dispute concerns the position of the Hauterivian/Barremian boundary. Bralower (1991) suggested that this may have been placed some 4m too high in the Speeton section (which would put it approximately at the *gottschei-marginatus* ammonite zonal boundary), but this proposal has been discredited herein. The presently available nannofossil data indicates that this stage boundary is currently (following Kemper *et al.*, 1981) placed slightly too *low* in the Speeton section, and should probably be raised to the top of the *variabilis* Zone. This younger placement agrees with Rawson's original (1971) boundary, and with the general positioning of the boundary in Germany (at the top of the *discofalcatus* Zone). The following nannofossil datums suggest this amendment:

(1) LOD of *Speetonia colligata* - Bergen (1994) places the LO of this unmistakable species confidently (T 10/10 sa) in the Upper Hauterivian *ligatus* Zone of S.E. France. This is a predominantly Tethyan species, with a high COR at low-latitudes - 94% at DSDP Site 534 (Bergen, 1994) and 95% at ODP Site 638 (from Applegate & Bergen, 1988). COR is much reduced at Boreal latitudes (43%), so the LOD of this species is likely older at these latitudes. *S.colligata* is rare towards the top of its range in the studied sections, but its LOD falls in precisely the same position in Speeton and Borehole 81/43,

just below the LOD of *C.maculosus* (upper BC 11b). This LO is centimetres below the top of the *marginatus* Zone at Speeton, i.e. it is virtually coincident with the Hauterivian/Barremian boundary as defined by Kemper *et al.*, 1981. Since this is a confirmed intra-Upper Hauterivian datum, it strongly suggests that the Hauterivian/Barremian boundary is placed too low at Speeton. Jakubowski (1987) recorded *S.colligata* from an unspecified horizon within the *variabilis* Zone of Speeton; this is not confirmed in the present study, despite very close sampling of this level, but, again, suggests that the Hauterivian/Barremian boundary should be raised.
(2) FOD of *Assipetra terebrodentarius* - This lies within the *variabilis* Zone of Speeton, and at a corresponding level in Borehole 81/43. Bergen (1994) reports this event in the latest Hauterivian *angulicostata* Zone of S.E. France, but may have included the light-microscopically similar *Rucinolithus windleyae* in his concept of this species (Bergen, *pers. comm.*). *R.windleyae* appears much earlier, in the mid-Hauterivian (this study), but occurs sporadically and may have been overlooked in Bergen's (condensed?) mid-upper Hauterivian sections. Thus, Bergen's FOD probably represents the genuine FO of *A.terebrodentarius*; in any case, it provides a conservative Late Hauterivian datum, and suggests that the *variabilis* Zone belongs in the Upper Hauterivian.

As with other fossil groups, Boreal-Tethyan correlation is difficult in the Barremian. Nevertheless, the following datums may be correlatable:
(1) LOD of *Haqius ellipticus* - this is in the *rarocinctum* Zone at Speeton, but is poorly defined (T 1/10 sa). Bergen (1994) reports this LO in the *hugii* Zone of the Barremian stratotype.
(2) LOD of *Tubodiscus jurapelagicus* - this is in the lower *fissicostatum* Zone of Speeton (T 3/10 sa). Applegate & Bergen (1988) recorded the LO of this species in the Barremian of the Galicia Margin, but Bergen (1994) included *Tubodiscus parvus* in his concept of the species, extending its range into the Turonian.
(3) LOD of *Cretarhabdus radiatus* - Bergen (1994) reports this datum (T 9/10 sa) in the late Early Barremian *moutonianum* Zone of the Barremian stratotype. My highest records of *C.radiatus* are in the *fissicostatum* Zone of Speeton (in which it is quite common). However, this species was not regarded as having marker potential, and its range might be extended by further checking. This datum might be useful for positioning the Lower/Upper Barremian boundary in Boreal sections.

Thus, although further checking is required, there is potential for inter-regional correlation within the Barremian. The Aptian is problematical, not because of a lack of potential datums, but due to a lack of complete, nannofossiliferous sections in which to calibrate the many FOs within this interval. *Hayesites irregularis*, which is widely used as a basal Aptian marker at low-latitudes (e.g. Bergen, 1994) has low COR in Boreal sections, and its FO is probably not a reliable datum. It is interesting that the markers

which Jakubowski (1987) used to zone the Aptian of the North Sea (*L.moray-firthensis* and *F.varolii*) have not been recorded from the Tethyan stratotypes, even though *F.varolii* is now known to be widely distributed (e.g. Varol, 1992). These species have probably been overlooked, or lumped with similar forms, in the less well-preserved Tethyan material.

Nannofossil species acmes have proven very useful in dating North Sea sections of Lower Cretaceous to Tertiary age (Jakubowski, 1987; Mortimer, 1987; Crux, 1989; Mutterlose, 1991a; Varol, 1989; this study). Similarly, the Quaternary can be zoned using a dramatic sequence of acmes that seem to be correlatable throughout the North Atlantic (Weaver & Hine, *in press*). Unfortunately, little abundance data has been published on the Tethyan Lower Cretaceous, so the geographical extent of acmes recognised in the North Sea remains uncertain. Based on limited data from the Barents Sea, the several acmes of *C.margerelii* may be correlatable this far north, but other acme-forming species (e.g. *Z.scutula*) may not have ranged to these latitudes. Given sufficient biostratigraphical control (using discrete F/LODs), it is possible that certain acmes may be correlatable with Tethyan sites.

CHAPTER 4:

PALAEOCEANOGRAPHY

4.1 - INTRODUCTION

Virtually all Cretaceous nannofossil species are long-extinct and their environmental preferences can only be gleaned indirectly. As with most fossil groups, many nannofossil species have restricted palaeobiogeographical distributions, and can thus be inferred to have been Tethyan/Boreal, warm/cold-water forms, low/high fertility indicators, etc.. However, if we consider the changing distribution of living coccolithophorid species (whose environmental preferences are relatively well-established) through the well-documented climatic upheavals of the Quaternary, it becomes apparent that considerable caution should be exercised when "labelling" a particular nannofossil and, more especially, when interpreting abundance data.

4.1.1 - Modern nannoplankton - spatial and temporal (Quaternary) distribution

The photosynthetic life-style of modern coccolithophores restricts them to the upper, euphotic zone of the world's oceans, and their distribution - both biogeographically and vertically within a given water column - is controlled by a variety of physico-chemical factors including light (duration and intensity), temperature, salinity, nutrient availability, and water column structure. All of these factors are inextricably interlinked - some clearly so (e.g. light and temperature, which are both largely determined by latitude), and others rather more cryptically. Thus, for example, upwelling regions of high nutrient availability are often characterised by relatively cool (deep oceanic) surface water that may be relatively opaque to light.

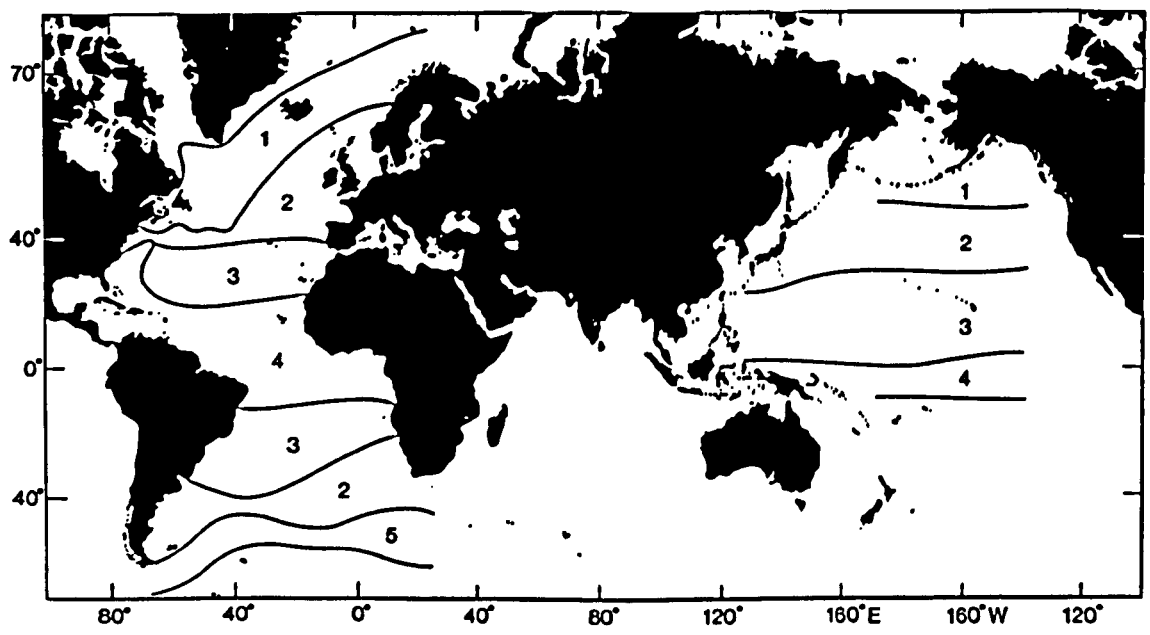


Fig. 4.1 - Modern biogeographical coccolithophore zones of the Atlantic and Pacific Oceans, from Winter *et al.*, 1994 (compiled from McIntyre & Bé, 1967 (Atlantic) and Okada & Honjo, 1973 (Pacific)).

The large-scale distribution of modern coccolithophores has been shown to be mainly temperature controlled, enabling the definition of broad, latitudinally defined biogeographical zones (Fig. 4.1). The majority of living species show a clear preference for warm-water, and are restricted to low and middle latitudes. There is thus a marked poleward decline in nannoplankton diversity. *Coccolithus pelagicus* and *Gephyrocapsa muellerae* are the only living species with clear cold-water preferences. *C.pelagicus* currently proliferates in subarctic waters and is virtually excluded from subtropical and warmer waters. However, this species is very rare at high southern latitudes where it underwent virtual regional extinction during the Holocene (McIntyre *et al.*, 1970; Gard, 1989); meanwhile it underwent massive proliferation in the northern North Atlantic, at a time of climatic warming (Gard, 1987). Thus, although *C.pelagicus* is obviously cold-water preferring, neither its current global distribution nor its temporal distribution can be easily explained in terms of climate (Gard, 1989). *Emiliania huxleyi* is the most ubiquitous and widely occurring modern coccolithophorid, and is tolerant of the entire temperature range encountered in today's oceans. This most cosmopolitan of species has dominated assemblages (often constituting >80%) since c.80,000 years B.P. (Thierstein *et al.*, 1977), when it underwent inexplicable proliferation. The remainder of the Quaternary is zoned using the acmes of several other species, e.g. *Gephyrocapsa aperta* and *Gephyrocapsa caribbeanica*, which Weaver & Hine (*in press*) conclude to be "independent of Quaternary climate change as demonstrated by their persistence throughout both warm and cold intervals." These acmes tend to mask the palaeoceanographically significant signals of environmentally sensitive species. Thus, Quaternary palaeoceanographers have resorted to plotting the ratios of temperature-sensitive species - e.g. the *G.oceanica:G.muellerae* (warm : cold) ratio - in order to remove the effect of time-progressive changes in nannofloral dominance (Weaver & Pujol, 1988; Hine, 1990). Even then their results have often been difficult to interpret - Hine (1990) concluded that "there is no direct linear relationship between the ratio of *G.oceanica:G.muellerae* and other proxy surface water indicators."

4.1.2 - Lower Cretaceous nannoplankton - problems in interpretation

As with living nannoplankton, temperature seems to have been the major factor controlling the distribution of Early Cretaceous nannofossils, and warm and cold-water species are readily identifiable by their palaeobiogeographical distributions. However, as in the Quaternary, environmentally induced variations in the abundance of the temperature-sensitive forms may be masked by time progressive nannofloral changes that are entirely unrelated (or perhaps cryptically related) to the prevailing palaeoceanographical conditions. The regionally correlatable acmes observed in the Lower Cretaceous are seldom as intense (in terms of total assemblage dominance) as those of the Quaternary but are much longer in duration, and may remain similarly

unexplained. Thus, plots of the relative or absolute abundance of a particular species over long time intervals are unlikely to be particularly meaningful; various studies have attempted such plots, even applying factor analysis to the results (Erba, 1986), but these have generally failed to draw any very meaningful conclusions. I have thus refrained from extensive plotting of abundance data - the chief reason for gathering such data was to enable identification of regionally correlatable acmes which, if they are to be useful, should be immediately recognisable from basic count data. I have, however, plotted detailed abundance data from short, closely-sampled intervals, which are unlikely to have been influenced by time-progressive changes.

A number of additional problems are specific to the Lower Cretaceous:

1. Palaeogeographical isolation - The North Sea basin was particularly susceptible to palaeogeographical isolation during the Early Cretaceous, when periodic lowering of sea-level resulted in closure of marine connections to the south. Thus isolated, and only connected to the southern oceans via rather tenuous northerly seaways (along proto-North Atlantic rifts, to the west of Ireland, and via the Russian Platform), immigration of stenothermal species from southern latitudes would have been impossible. These sea-level events were undoubtedly related to palaeoclimate, but the exact relationship is uncertain. Thus, depending on the climatic regime during the period of isolation, a number of quite different scenarios are possible - isolation under favourable conditions might have resulted in proliferation and development of endemic forms, while isolation under unfavourable conditions might have caused regional extinction.

2. Incomplete record - Due to a number of major sea-level events, most Lower Cretaceous sections are very incomplete, and subject to differential condensation. This makes detailed comparison of assemblages over long time intervals difficult.

3. *Incertae sedis* forms - *Nannoconus* and *Tegulalithus*, for example, have no obvious living analogues and may have had very different life-cycles to modern coccolithophorids.

4. Taxonomic concepts & lumping - Another lesson to be learnt from Quaternary studies is that excessive taxonomic lumping is undesirable: the two most environmentally useful species of *Gephyrocapsa* - *G.muellerae* and *G.oceanica* (representing cold and warm-water forms, respectively) - were, until very recently, lumped together by many workers. Thus the lumped categories of most Cretaceous palaeoceanographers should be regarded with some suspicion; several of the most commonly used "species" (e.g.*"B.constans"* and *"Z.erectus"*) are clearly polyspecific. Inconsistent taxonomic concepts make comparison of different authors data difficult.

4.2 - PREVIOUS PALAEOCEANOGRAPHICAL STUDIES

With the realisation that nannofossil zonation schemes were limited in their geographical applicability, Cretaceous nannopalaeontologists were forced to confront the problem of provincialism. Documentation of this phenomenon formed the basis of subsequent palaeoceanographical studies. The main palaeoceanographical studies dealing with lower-middle Cretaceous nannofloras are summarised below.

AUTHOR	PRINCIPAL OBSERVATIONS
Thierstein, 1976	Low-high latitudinal differentiation.
Wise & Wind, 1977	Distinct high southern latitude flora (Austral province).
Roth & Bowdler, 1981	Neritic-oceanic differentiation.
Roth, 1981	Increased abundance of *Z.erectus* & *B.constans* towards palaeo-upwelling zones (- "high fertility forms")..
Roth & Krumbach, 1986	Fertility preferences confirmed (?) by factor analysis.
Erba, 1986, 1987; Premoli-Silva, *et al.*, 1989	*B.constans* & *Z.erectus* most abundant in black shales (high fertility); *Nannoconus* spp. most abundant in limestone.
Erba, 1989	*Nannoconus* distribution
Busson & Noël, 1991	*Nannoconus* distribution
Coccioni *et al., in press*	Distributions of *Z.erectus* and *Nannoconus* spp. across an anoxic event (OAE1a) seem to confirm eutrophic & oligotrophic preferences, respectively.
Erba, 1992	*B.constans* & *Z.erectus* (="high fertility indices") become increasingly abundant at Pacific sites as they drift towards the palaeoequatorial upwelling zone; *B.constans* responds to increased fertility before *Z.erectus*.
Erba *et al.*, 1992	Spectral analysis shows cyclical variation in the abundance of *B.constans* and *Z.erectus* (="high fertility indices") at Milankovitch periodicities (obliquity & eccentricity), although these are out of phase. Distribution of *W.barnesae* (= low fertility index?) is inversely related to that of *B.constans*.
Watkins, 1989	Assemblage diversity is related to environmental stability. In chalk-marl rhythms the marls yield low diversity assemblages with more abundant *Z.cf.erectus* & *B.constans* (-unstable, meso/eutrophic conditions); the chalks yield more diverse assemblages that are depleted in "high fertility indices" (-stable, oligotrophic conditions).
Mutterlose & Harding, 1987	Influxes of *Nannoconus*, *Conusphaera*, and *D.rectus* to the Boreal area during periodic warm-water ingressions
Mutterlose, 1988	The distribution of Boreal & Tethyan-derived nannofossils within the Ryazanian-Hauterivian of the Boreal Realm is comparable with the distributions of macrofossils & foraminifera.
Mutterlose, 1989a	High abundances of *Nannoconus* spp. and *R.asper* in the mid-Aptian of both the North and South Atlantic are indicative of transgression +/- climatic warming.
Mutterlose, 1991b	*Nannoconus* spp., *Micrantholithus* spp. & *C.rothii* are restricted to the pale horizons (presumed to have been deposited under warmer conditions) in pale-dark rhythmic sections.
Mutterlose, 1992a	Bipolar distribution of *C.salebrosum*.

Thomsen, 1989	Monospecific assemblages in the finely-laminated Munk Marl Bed reflect seasonal blooms. *Biscutum* spp. is the only taxon to be evenly distributed throughout a succession of laminae.
Applegate *et al.*, 1989	Major assemblage differences between the North Sea & northern Tethys reflect substantial palaeogeographical barriers.
Cooper, 1989	Relatively weak differentiation of Boreal & Tethyan Realms during the Kimmeridgian to Valanginian (75% of species common to both). No significant decrease in diversity in higher latitude.
Crux, 1989	The distribution of Boreal & Tethyan nannofossils within the Neocomian of N.W. Europe is consistent with the patterns of cephalopod migration and sea-level events. *R.asper*, *C.margerelii* & *D.lehmanii* (= *A.jakubowskii*) are especially abundant during transgressive intervals.
Crux, 1991	Direct inter-regional correlation is possible in the Mid-Upper Albian, due to continuous marine connections. Acmes of *R.parvidentatum* and *S.primitivum* related to climatic cooling.

4.3 - APPRAISAL OF PREVIOUS WORK

Most of these studies, and virtually all those on oceanic sites, have concentrated on the mid-Cretaceous (Albian-Cenomanian), when both the species composition and the layout of the world's oceans were very different to the Neocomian. Thus, it follows that the environmental preferences established therein may not be applicable in older, Neocomian intervals; this is especially true in the case of long-ranging but poorly-defined species such as *B.constans* and *Z.*cf.*erectus*, which have formed the mainstays of a number of studies. Most studies have tried to explain the observed nannofloral changes in terms of either sea surface temperature or surface water fertility - the effects of these two, major variables are considered below.

4.3.1 - Sea Surface Temperature

The palaeobiogeographical distributions of many taxa are clearly demarked by palaeolatitude, and hence related to palaeotemperature (in all subsequent discussion temperature is taken to mean *sea surface* temperature; bottom water temperature is relatively constant). Thus, warm and cold-water species were readily identified. As at present, a number of species were entirely restricted to a broad circum-equatorial belt (e.g. *Calcicalathina oblongata*), only very occasionally making incursions to higher, "temperate" latitudes. Such incursions might reflect climatic warming or increased basin connectivity, or a combination of these factors. Certain high-latitude species appear to have been restricted to one hemisphere (thus Boreal and Austral provinces have been differentiated), while other such species had bipolar distributions (e.g. *C.salebrosum*). As demonstrated in the Quaternary, it does not follow that bipolar species must have concurrent ranges in both hemispheres, although such diachroneities might be relatively insignificant on a much longer, geological time scale.

Lower Cretaceous nannofossil species exhibiting strong palaeotemperature preferences are compiled in the list below; the warm-water preferring species are listed in approximate order of their degree of limitation (i.e. most stenothermal species first). Those species listed as having cryptic environmental preferences have unusual or disjunct distributions that are not readily explained. Various other species, previously regarded as cool-water, 'Boreal' forms have recently been found to be widely distributed.

Warm-water preferring	Cool-water preferring	Cryptic preferences
Calcicalathina oblongata	*Crucibiscutum salebrosum*	*Watznaueria britannica*
Lithraphidites bollii	*Seribiscutum primitivum*	*Zebrashapka vanhintei*
Cruciellipsis cuvillieri	*Repagulum parvidentatum*	*Pickelhaube furtiva*
Zeugrhabdotus erectus	*Sollasites arcuatus*	*Clepsilithus maculosus*
Zeugrhabdotus xenotus		*Diloma galiciense*
Helenea quadrata		
Rhagodiscus infinitus		
Percivalia fenestrata		
Speetonia colligata		
Nannoconus spp.		

4.3.2 - Surface Water Fertility

The recent documentation of Oceanic Anoxic Events (OAEs) in the Cretaceous has led to considerable interest in fertility/productivity indices. Perhaps because of this sudden interest, the importance of surface water fertility to Cretaceous nannoplankton may have been exaggerated.

High surface water fertility results from upwelling of nutrient-rich water from depth. Persistent upwelling is essentially wind-driven, and occurs in two main situations - along suitably oriented coasts and at oceanic divergences (Parrish & Curtis, 1982). Coastal upwelling occurs when a longshore wind and the effect of the rotation of the earth (Coriolis effect) combine to create a net offshore flow of water in the upper water column; this is replaced by deeper water, from below the photic zone, that is relatively nutrient-rich. Such upwelling occurs today along the western margins of continents. Oceanic divergences occur under persistently low atmospheric pressure, where outflowing of surface water causes upwelling from shallow depths; such regions occur today along the equator, around Antarctica, and in subarctic waters.

The distributions of modern coccolithophores are not clearly limited by surface water fertility, and low/high fertility indicating species are not obviously identifiable. In a recent study of the Late Quaternary nannofloras of a permanent upwelling cell, Jordan *et al.* (*manuscript*) conclude that "it is not known with any certainty whether coccoliths can be used to identify palaeo-upwelling events within marine sediments." Eutrophication (either seasonal or year-long, depending on the setting) results in high standing crops of coccolithophores and diatoms, but the species composition of the coccolithophores is still determined largely by temperature. Thus, eutrophication of tropical, temperate and sub-arctic waters results in increased absolute frequencies of *Gephyrocapsa oceanica*, *Emiliania huxleyi* and *Coccolithus pelagicus*, respectively. An additional complication is that the eutrophic surface waters of upwelling regions may contain a relatively high proportion of cold-water forms (e.g. *Gephyrocapsa muellerae*), since upwelling (deep oceanic) water is relatively cool.

Roth (1981) was first to record the influence of fertility on Cretaceous nannoplankton. He recorded elevated abundances of *Z.erectus* and *B.constans* at inferred palaeo-upwelling regions (along a Pacific palaeoequatorial divergence zone and the eastern margins of the Atlantic), and proposed that these taxa preferred conditions of high surface water fertility. However, Roth's data-set was extremely limited, utilising only very few "best preserved" samples that were not even roughly contemporaneous (biostratigraphical control was limited at this time). Roth & Bowdler later (1986) "confirmed" these fertility preferences using a slightly larger sample set, with similarly limited biostratigraphical control. These authors also noted a negative correlation between the abundance of *Watznaueria barnesae* and their high fertility forms, inferring a low fertility preference for this dissolution-resistant species. The minimal data-bases of these early palaeoceanographical studies cannot be overemphasised - in a number of instances the assemblages of particular sites were characterised by single samples, that were judged to be representative of a "time slice" spanning perhaps 10 Ma. Bearing in mind the dramatic temporal variations in assemblage composition that are known to occur, the results of these studies should be regarded with caution. Nevertheless, the "fertility preferences" proposed therein have formed the basis of numerous subsequent palaeoceanographical studies (Erba, 1986, 1987, 1992; Erba *et al.*., 1992; Premoli-Silva, *et al.*, 1989; Watkins, 1989; Coccioni *et al.*, *in press*). The results of these studies may be summarised as follows:

(1) *B.constans* and Z. cf.*erectus* show similar, but out of phase fluctuations in abundance, and are often associated with organic-rich deposits.

(2) The distributions of these small species are often inversely related to those of *W.barnesae* and *Nannoconus* spp.; the latter taxon shows a preference for carbonate-rich horizons.

Taxonomic clarification may provide a partial explanation of these phenomena. *B.constans*, *Z.erectus* and *W.barnesae*, as used in palaeoceanographical studies, are all clearly polyspecific. *B.constans* is applied to a number of small species of *Biscutum*, that are difficult to resolve on the LM. Similarly, *Z.erectus* has been used for various, small (<5μm long) species of *Zeugrhabdotus*, of which *Z.noeliae* is the most common. *W.barnesae*, as applied by most authors, is probably the most ill-defined of these taxa (including *W.barnesae*, *W.communis*, *W.fasciata*, *W.fossacincta*, etc.). Thus, each of these categories is likely to contain several species, that may have had quite different environmental preferences. The resultant, smoothed palaeoceanographical signals are unlikely to retain much primary significance. Cyclical, Milankovitch scale fluctuations in the relative abundance of these "species" might be induced by orbitally driven variation in the abundance of a single, dominant taxon. The inverse relationship between the abundance of *W.barnesae* and *B.constans*, observed in a number of studies, may be due to the contrasting preservation potential of these taxa, or to the "closed sum" effect, whereby variations in the abundance of one taxon cause changes in the relative abundance of the other.

In any case, the fertility preferences of nannofossils cannot be proven until we decide what constitutes evidence of fertility; the actual recognition of palaeoproductivity from the sedimentary record is problematical. Numerous proxies have been used to determine palaeoproductivity, but differentiation of primary productivity (= overall organic production, reflecting the availability of nutrients at the sea surface (= fertility)) and carbonate productivity (= the production of calcareous plankton) remains problematical. The relative proportions of carbonate and organic carbon are, of course, heavily dependant upon other factors as diagenesis and the amount of terrigenous input (which depends on sea-level, climate, and palaeogeographical setting).

Basin stagnation, with formation of anoxic bottom water, has generally been invoked to explain the formation of organic-rich sediments; limited circulation results in stratification of the water column, bottom water anoxia, and consequent high preservation of organic matter. However, Pederson & Calvert (1990) suggest that high primary productivity, rather than bottom water anoxia, is the primary control on the accumulation of organic-rich sediments. These authors quote the example of the Black Sea - the sediments presently accumulating under an anoxic water column are not particularly enriched in organic matter, but an extremely organic-rich sapropel was deposited during the Holocene at a time when the basin was oxic. They further suggest that oceanic circulation during the Cretaceous was similar to or more intense than modern conditions, despite the more equable climate, and that the widespread deposition of black shales during the lower-middle Cretaceous resulted from temporal and spatial increases in primary

production, rather than from OAEs brought about by sluggish circulation. Thus, the whole issue of palaeoproductivity remains contentious.

4.4 - CONSIDERATION OF THIS STUDY'S ASSEMBLAGE DATA

4.4.1 - Spatial variation of assemblages

The studied sections span an approximately north-south transect of >2000km, across >20° of palaeolatitude, and are thus much more disparate than English or German basins were from northern Tethys. The sites are thought to have been well connected via a branch of the proto-North Atlantic throughout the studied interval, so assemblage differences should reflect environmental conditions (most likely a latitudinal temperature gradient) rather than palaeogeographical isolation. Most of the marker species utilised in North Sea sections were recorded in the Barents Sea, enabling confident dating of these sections. Condensation and patchy preservation limit the extent of any comparison, but the following observations can be made.

(1) ***Crucibiscutum salebrosum.*** The most striking assemblage difference is the increased abundance of *C.salebrosum* at more northerly sites, compared to Speeton (Fig. 4.2). This species has a well-documented bipolar distribution (Mutterlose, 1992a), and has not been recorded from low-latitude sites. *C.salebrosum* is most abundant in Core 7B, offshore mid-Norway, where it constitutes up to 70% of basal Valanginian assemblages. The decreased relative abundance of this species at the Barents Sea sites probably reflects the relatively poor preservation of these assemblages; *C.salebrosum* has a much lower preservation potential than *Watznaueria* spp..

(2) ***Nannoconus* spp.**
(a) Ryazanian-Hauterivian - Nannoconids, which often dominate the Neocomian assemblages of Tethyan regions, occur only sporadically throughout the Ryazanian-Hauterivian of North Sea sections (Speeton and Borehole 81/43), never constituting more than about 2% of assemblages; only in the Barremian do they become conspicuous. However, *Nannoconus* occurs consistently throughout the incomplete Ryazanian-Hauterivian of Core 7B, offshore mid-Norway, attaining abundances of >10% in the basal Valanginian; this interval of peak abundance is, however, barren of nannofossils in the North Sea sections, so no direct comparison is possible. Thus, although nannoconids are much depleted in abundance relative to Tethys, they did not, apparently, undergo a progressive northward decline within the Boreal seaway, and may, in fact, have been more abundant offshore mid-Norway. The relatively high abundance of *Nannoconus* offshore mid-Norway might reflect the relatively close connection of this area to the

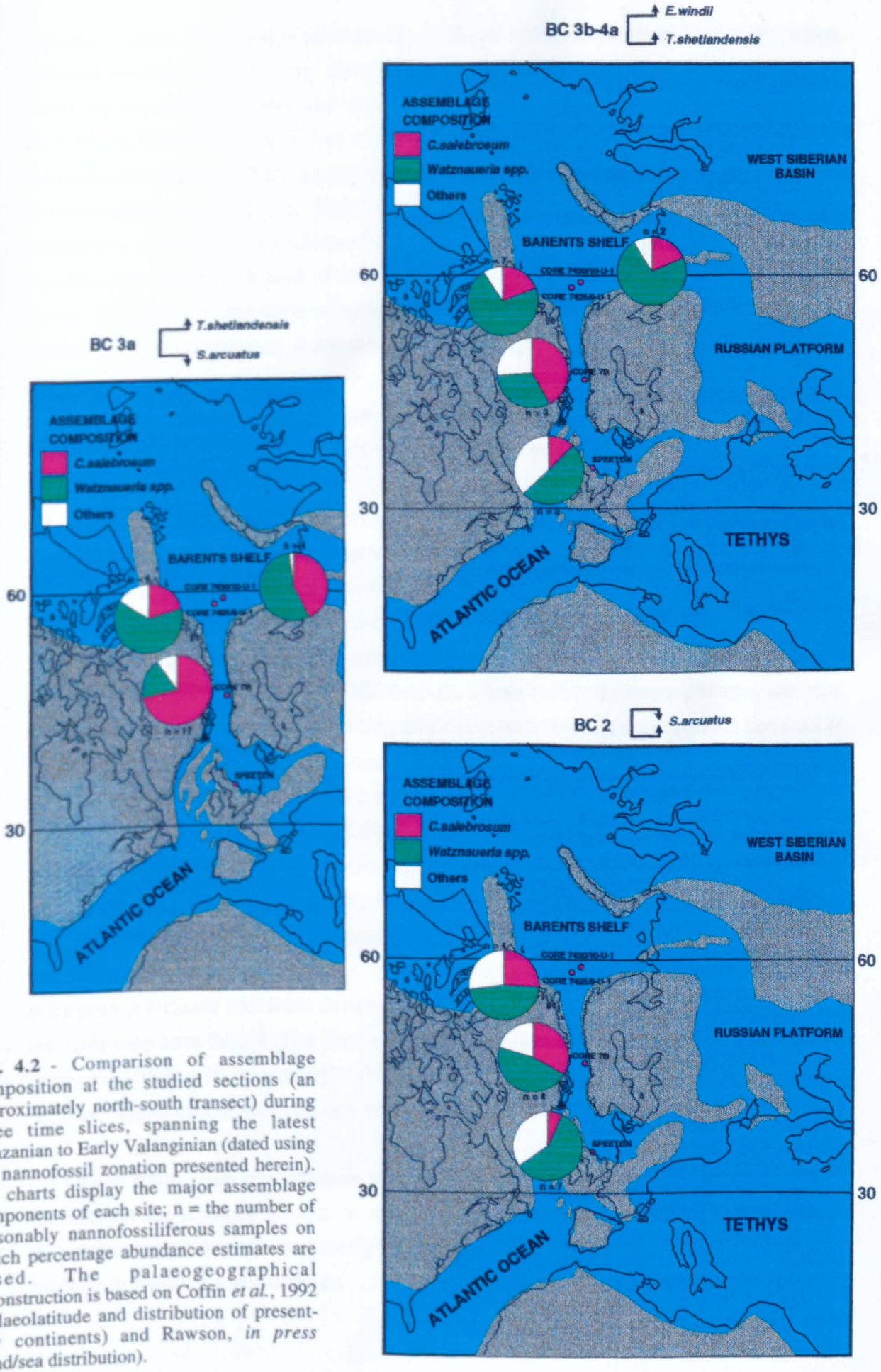


Fig. 4.2 - Comparison of assemblage composition at the studied sections (an approximately north-south transect) during three time slices, spanning the latest Ryazanian to Early Valanginian (dated using the nannofossil zonation presented herein). Pie charts display the major assemblage components of each site; n = the number of reasonably nannofossiliferous samples on which percentage abundance estimates are based. The palaeogeographical reconstruction is based on Coffin *et al.*, 1992 (palaeolatitude and distribution of present-day continents) and Rawson, *in press* (land/sea distribution).

PAGE

NUMBERING

AS ORIGINAL

Atlantic Ocean, along rifts between the U.K. and Greenland (see Fig. 4.2); warm, Atlantic sourced currents may have promoted nannoconid proliferation. It should be noted that the earliest Valanginian nannoconid assemblages of Core 7B are dominated by an endemic Boreal species, *N.oviformis*. This species probably accounts for the bulk of the carbonate of the basal Valanginian limestone, considering its very large size relative to the coccoliths constituting the remainder of the nannoflora (these are dominated by the diminutive *C.salebrosum*). Contemporaneous assemblages from the Barents Sea are, significantly, entirely devoid of nannoconids, despite the favourable, carbonate-rich facies. The Barents Sea carbonates were deposited in clear, shallow water of normal marine salinity - conditions under which *Nannoconus* proliferated elsewhere - thus the limiting factor precluding nannoconids from this area must have been temperature. It seems that, under the climatic conditions of the Ryazanian-Hauterivian, the northern limit of *Nannoconus* lay somewhere between mid-Norway and the Barents Shelf.

(b) Barremian - Nannoconids underwent considerable proliferation, and diversification, during the Early Barremian *rarocinctum* Zone (Speeton, Borehole 81/43 and Germany), and remained important nannofloral components throughout the Early Barremian in the North Sea area (see Fig. 4.4). In addition, it seems that they first colonised the Barents Shelf during the early-middle Barremian (they account for up to 7% of dissolution-modified assemblages in Core 7430/10-U-1). These rather dramatic changes are best explained in terms of climatic warming and basin isolation - isolation under favourable (warm) conditions would have caused proliferation, with the development of endemic forms (*N.abundans* and *N.borealis*), while a more equable climate would have allowed colonisation of the Barents Shelf. Facies changes in marginal basins and endemism among ammonites indicate regression and isolation of the North Sea basin during the Barremian (Fig. 4.3), while clay mineralogical and other sedimentological evidence has recently indicated the existence of a Barremian "arid phase" (Ruffell & Batten, 1990). Aridity (= low rainfall), temperature, and sea-level are all intimately related, but the exact relationship remains uncertain. It has been suggested (A. Ruffell, *pers. comm.*) that arid intervals may have been cooler than humid intervals, but this is by no means certain, and seems to conflict with the nannofloral evidence. Whatever the exact climatic expression of "aridity," nannoconids seem to have enjoyed these conditions.

(3) **Other taxa.** Poor preservation and condensed sections in the Barents Sea might account for the absence of rare, or short-ranging species, but the reduced assemblage diversities cannot be explained solely by preservation. The following comparisons can be made with North Sea assemblages:

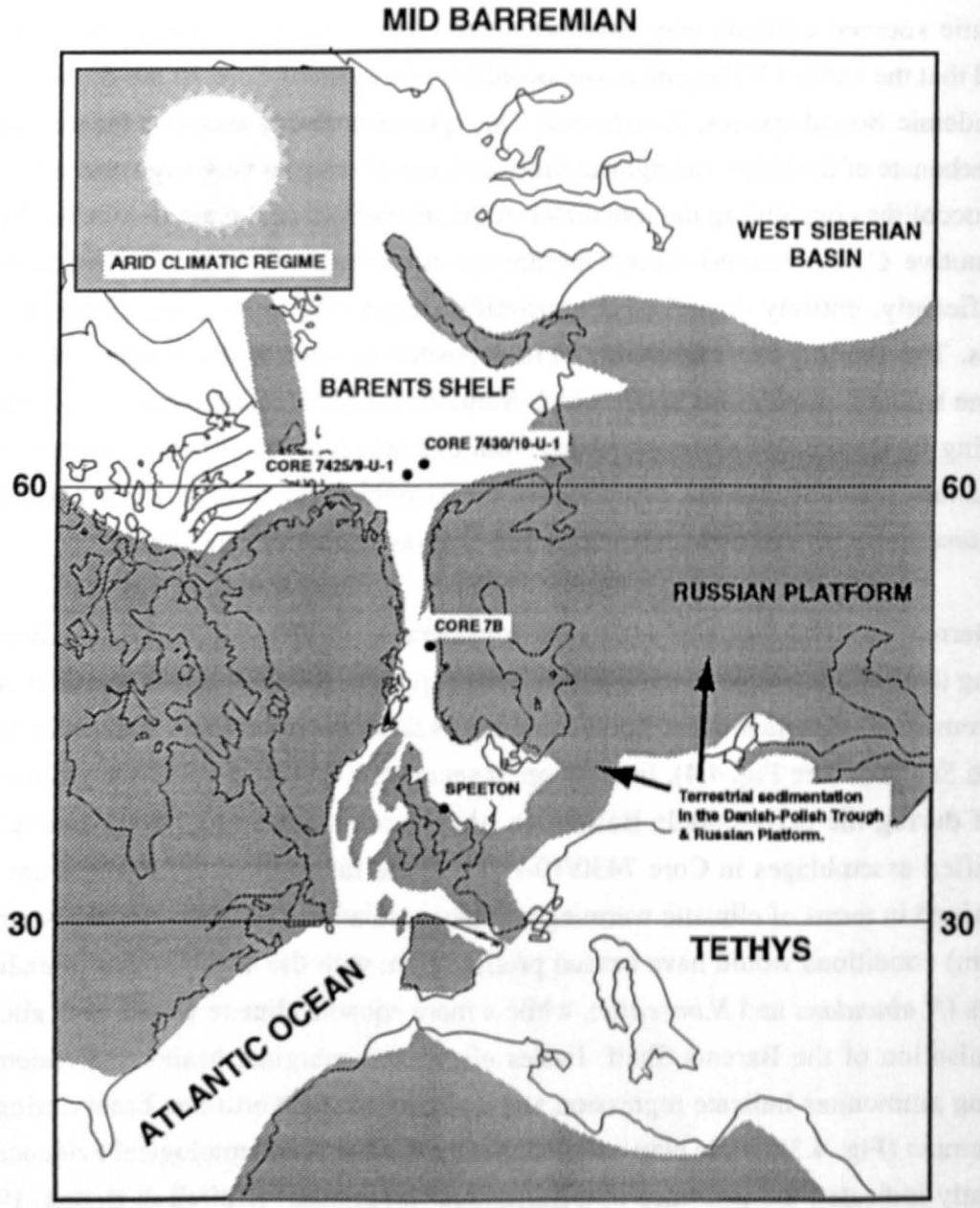


Fig. 4.3 - Tentative mid-Barremian palaeogeography. Based on Coffin *et al.* (1992) and Rawson (*in press*). Note the isolation of the North Sea basin, with all southerly connections to Tethys closed.

Important (marker) species present in the Barents Sea - *Conusphaera rothii*, *Crucibiscutum salebrosum*, *Eiffellithus striatus*, *Nannoconus abundans*, *Radiolithus antiquus*, *Rhagodiscus pseudoangustus*, *Tegulalithus septentrionalis*, *Perissocyclus plethotretus*, *Sollasites arcuatus*, *Triquetrorhabdulus shetlandensis*.

Taxa notably absent in the Barents Sea (asterisks indicate that incomplete stratigraphical coverage might account for non-recovery) - *Assipetra terebrodentarius**, *Clepsilithus maculosus**, *Cruciellipsis cuvillieri**, *Diloma* spp., *Grantarhabdus meddii*, *Helenea* spp., *Micrantholithus speetonensis**, *Speetonia colligata*, *Zeugrhabdotus scutula*.

Taxa that are markedly reduced in abundance (rare) in the Barents Sea - *Axopodorhabdus dietzmannii, Tubodiscus parvus, Zeugrhabdotus noeliae.*

Taxa that are more abundant (relatively) in the Barents Sea - *Crucibiscutum salebrosum, Cyclagelosphaera papilla, Zeugrhabdotus trivectis.*

Thus, there does seem to be a northward decline in nannofloral diversity, but this is probably less severe than that displayed by modern nannoplankton across similar latitudes (McIntyre & Bé, 1967, and *pers. ob.*). This might be expected, since the Cretaceous was a warm, equable period (Barron, 1983), with reduced global temperature gradients and ice-free polar seas.

4.4.2 - Long-term, stratigraphical variation of assemblages

Williams and Bralower (*manuscript*) have recently conducted a detailed, quantitative comparison of the nannofossil assemblages of Speeton, Borehole 81/43, and Gott, comparing both absolute and relative abundance data with carbonate content and stable isotopic ratios. They interpret long-term assemblage changes in terms of varying surface water fertility, possibly related to changes in sea-level. Their stable isotopic results do not correlate with observed assemblage changes, and might be explained largely by diagenetic alteration. However, this study is hampered by broad taxonomic concepts - only nine taxa, most of them lumped groupings, are considered in detail and several key taxa (e.g. *C.salebrosum* and *C.margerelii*) are not considered at all. In addition, the biostratigraphical control is slightly inaccurate (in particular, the short mid-Valanginian section in Borehole 81/43 is misassigned to the Lower Hauterivian, and Crux's (1989) *S.compitus* Zone (= BC 11) is inferred to exist, but not proven, in the lower part of the Gott section).

A detailed, quantitative comparison of assemblages is beyond the scope of the present study but, if rigorous taxonomy is applied, the acmes of many species correlate very well across the North Sea basin. Fig. 4.4 displays the relative abundance of major taxa in the Speeton section; very similar patterns are observed in Borehole 81/43 and Germany, if allowances are made for differential condensation and non-exposure. This plot illustrates the probable futility of drawing detailed palaeoceanographical conclusions from relative abundance data collected over long stratigraphical intervals. Several relatively major taxa became extinct during this interval (*C.salebrosum* and *T.septentrionalis*; the latter originating and becoming extinct within the unexposed section), while other important taxa originated (e.g. *N.abundans* and *Z.scutula*). Thus, the whole pattern of inter-specific competition changed several times during deposition of this section.

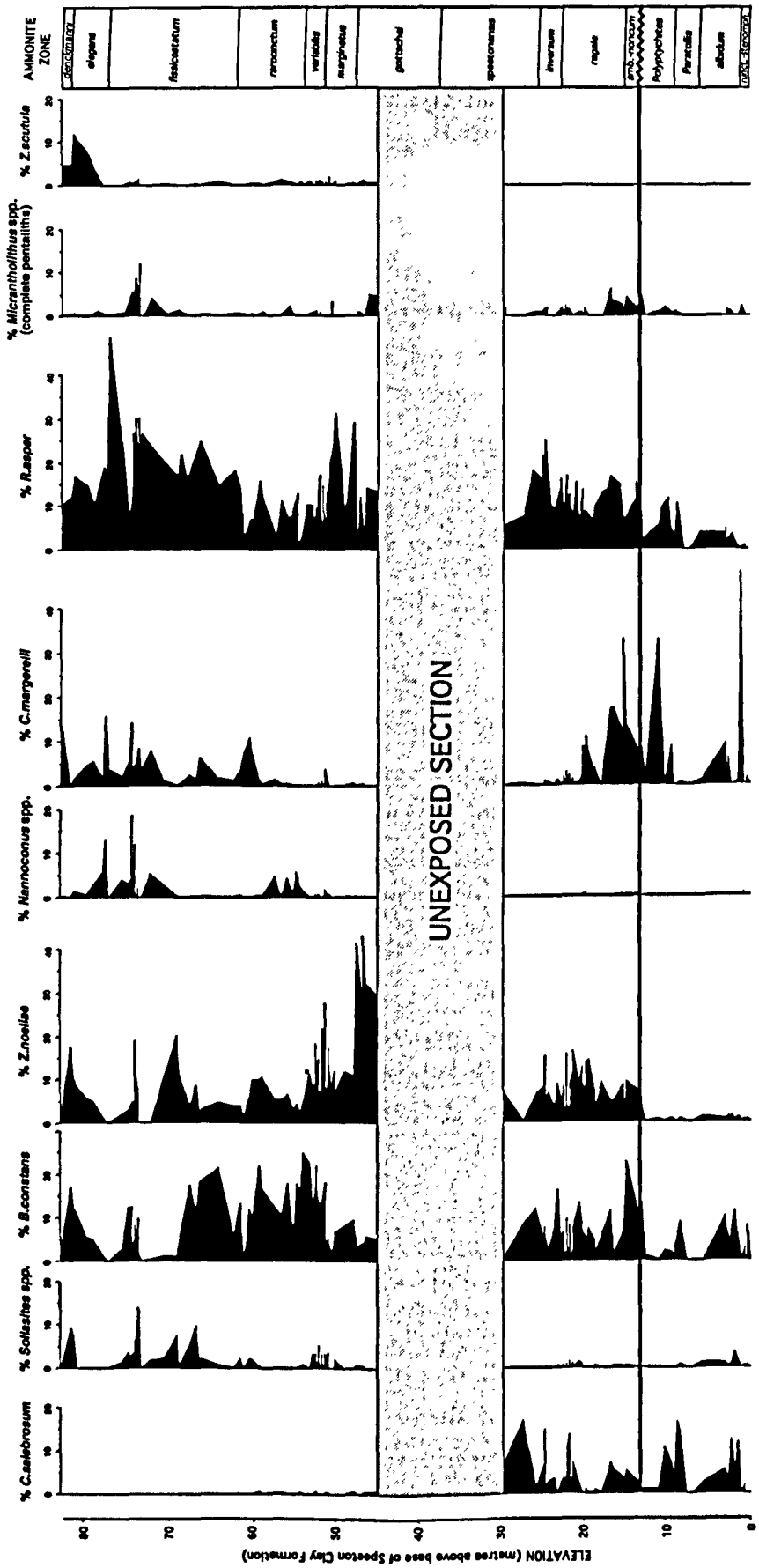


Fig. 4.4 - Relative abundance of major taxa in the Speeton section.

Nevertheless, certain very distinctive groups, e.g. the nannolith genera *Nannoconus* and *Micrantholithus*, probably retained broadly similar palaeoecological preferences throughout their evolutionary histories. *Nannoconus*, as a genus, displays a clear preference for warm water, and its proliferation in the Early Barremian is suggestive of climatic warming. However, these Early Barremian nannoconids are endemic, Boreal forms that might have been better adapted to life in cooler water. Similarly, the basin-wide acmes of long-ranging species such as *C.margerelii* and *Z.noeliae* probably hold some environmental significance. *C.margerelii* forms discrete acmes in the Upper Valanginian-Lower Hauterivian and in the Lower Barremian; the former acme is associated with the occurrence of strictly Tethyan taxa (e.g. *C.oblongata*, *C.cuvillieri*), while the latter is associated with the proliferation of nannoconids. Thus, *C.margerelii* might be a warm-water preferring taxon, but its occurrence in the Barents Sea, and peaks during other intervals lacking Tethyan influence (e.g. Bed D7A, at Speeton) suggest a more complex palaeoecology. High abundances of *B.constans* and *Z.noeliae* have been widely used to infer conditions of increased surface water fertility, but their fluctuations are out of phase (Fig. 4.4) and could be variously interpreted. As in the Quaternary, such long-term fluctuations in abundance may have been induced by evolutionary pressures, independently of environmental conditions. Thus, it is urged that restraint be exercised when interpreting abundance data - it is easy to jump to conclusions concerning surface water fertility, etc., but very difficult to prove such inferences one way or the other.

4.4.3 - Short-term variation of assemblages

Detailed quantitative examination of short stratigraphical intervals, in which assemblages are unlikely to have been affected by evolution-related, time-progressive changes, is more likely to yield useful palaeoecological information. Short sections displaying evidence of climatic variation (e.g. rhythmic bedding) could be especially useful in this respect. Three such sections were examined in the present study:

Pale/dark rhythmic section (Figs. 4.5-4.7)

This short (1.75m), rhythmically-bedded section spans the *marginatus-variabilis* ammonite zonal boundary at Speeton (= the Hauterivian-Barremian boundary, as currently defined there). The section exhibits striking pale/dark alternations in clay colour, that are thought to be palaeoclimatically related (they may record Milankovitch frequency climatic variations).

These bedding rhythms could be explained by changes in precipitation affecting the amount of terrigenous input, which would result in varying dilution of biogenic

carbonate. However, nannofossil abundance is relatively high throughout this section (with 40-100 specimens per field of view), and does not vary significantly between pale and dark beds (Fig. 4.5). This suggests that the bedding rhythms cannot be explained in terms of a simple "dilution" model.

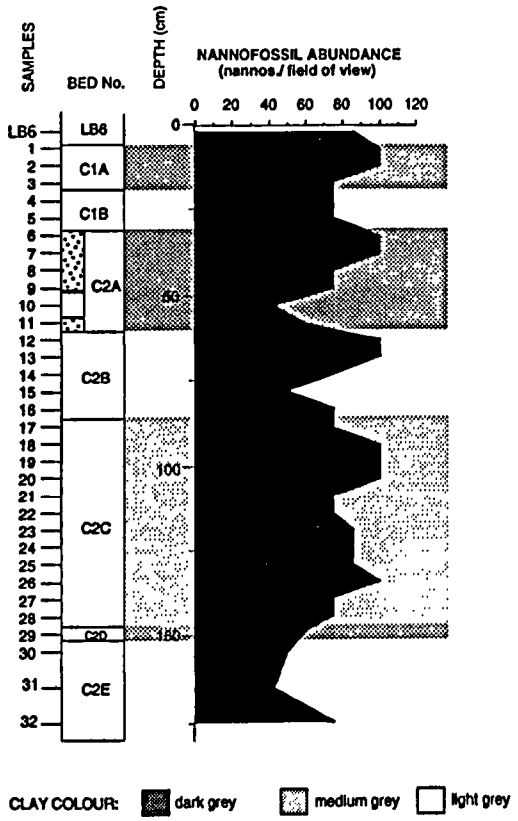


Fig. 4.5 - Total abundance of nannofossils through the pale/dark rhythmic section, roughly estimated in terms of the number of specimens per average field of view (at 1,250x magnification).

Previous authors have demonstrated that nannoconids are much more abundant in, or entirely restricted to, the carbonate-rich horizons of such rhythmically-bedded sequences (e.g. Erba, 1986, 1987; Mutterlose, 1991a). Thus, the carbonate-rich beds are presumed to have been deposited under warmer conditions. Nannoconids are rare in this studied interval (Fig. 4.6b), but are slightly more common in the paler beds; however, thorough checking of slides revealed their presence in every bed.

The "high fertility indices," *B.constans* and *Z.noeliae*, exhibit in-phase fluctuations in abundance, but show no clear preference for pale or dark horizons (Fig. 4.6a). In the lower part of Bed C2A, there is a sharp increase in the relative abundance of large *Watznaueria* spp. and *R.asper*, with a corresponding decrease in abundance of smaller, dissolution prone taxa (e.g. the "high fertility" forms); this is due to etching at this level, but preservation throughout the rest of the section is good, and abundance fluctuations are believed to be of primary (rather than diagenetic) origin.

Most of the species of *Watznaueria* recognised in this study would have been lumped together under *"W.barnesae"* by other workers, but these show quite different distributions within this section (Fig. 4.7). Some of these forms are probably ontogenetically-related, representing growth stages of a single species (Young & Bown, 1991), but the dominant type, *W.?fasciata*, is almost certainly a separate species, and displays a very different distribution to other, larger species of *Watznaueria.* Analogy with the modern genus *Gephyrocapsa* shows that even very similar species can have very different ecological preferences - if the numerous, but rather similar, species of *Gephyrocapsa* occurred in more diverse, Cretaceous assemblages, they would undoubtedly have lumped together as a single taxon for LM purposes. Thus, the "low fertility" preferences of *"W.barnesae"* inferred in several previous studies should regarded with caution. *A.jakubowskii*, *Apertasphaera* sp. and *D.ignotus* show interesting fluctuations in abundance through this section but, again, these are difficult to interpret.

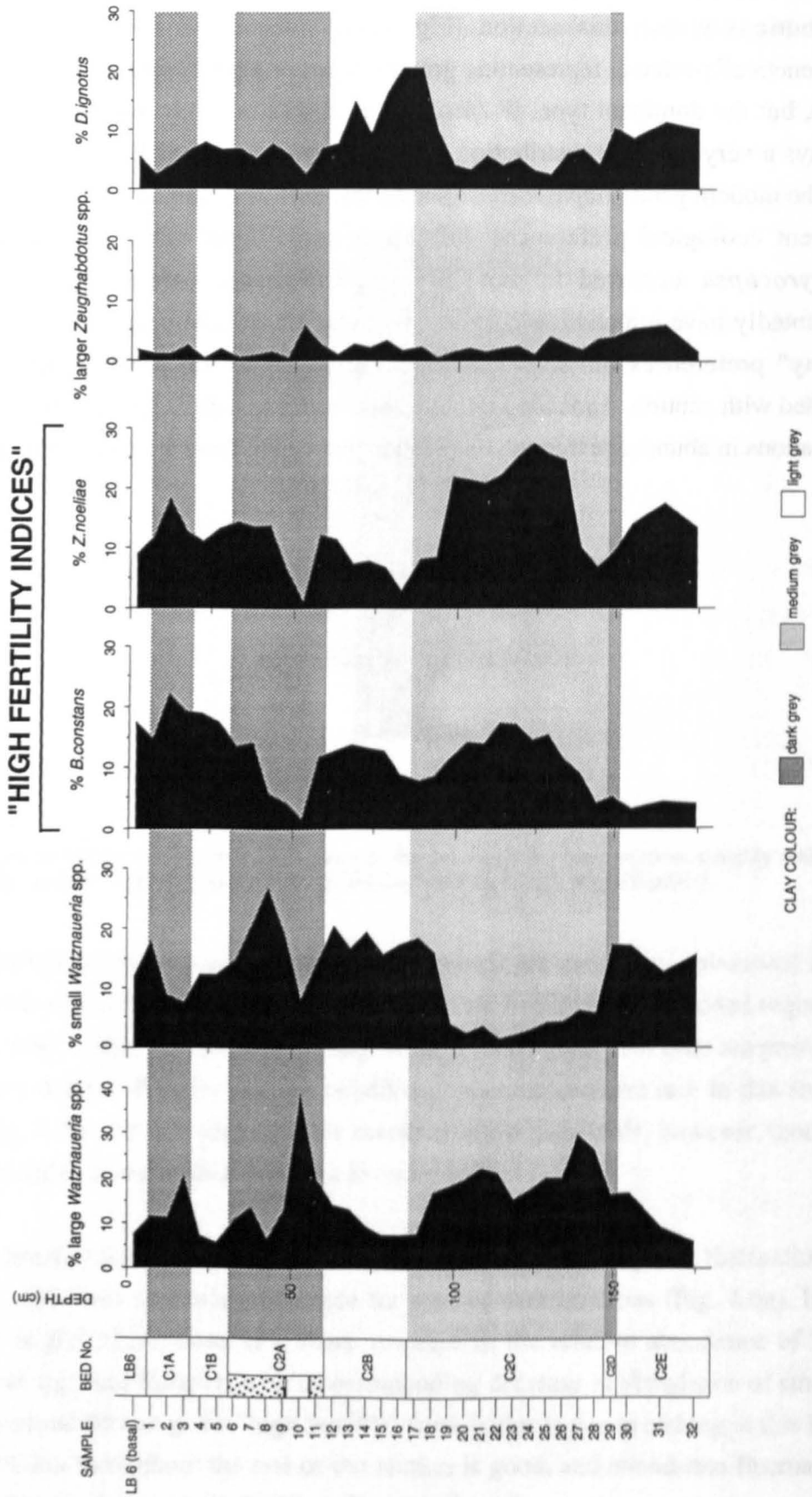


Fig. 4.6a - Relative abundance of main nannofossil taxa through the pale/dark rhythmic section. Small *Watznaueria* spp. includes *W.?fasciata* and *W.?rawsonii*; large *Watznaueria* spp. includes *W.barnesae*, *W.communis* and *W.fossacincta*.

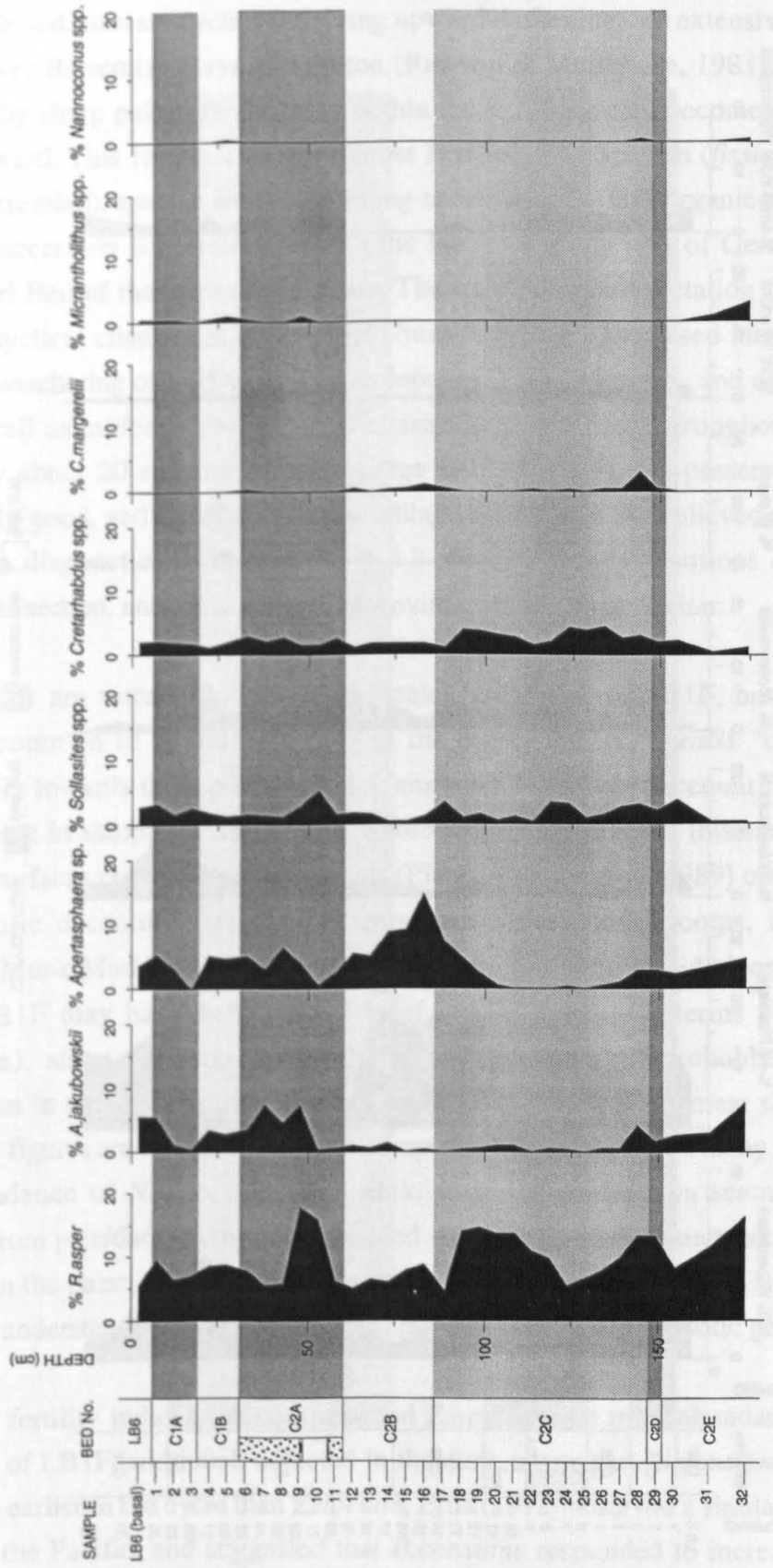


Fig. 4.6b - Relative abundance of main nannofossil taxa through the pale/dark rhythmic section (continued).

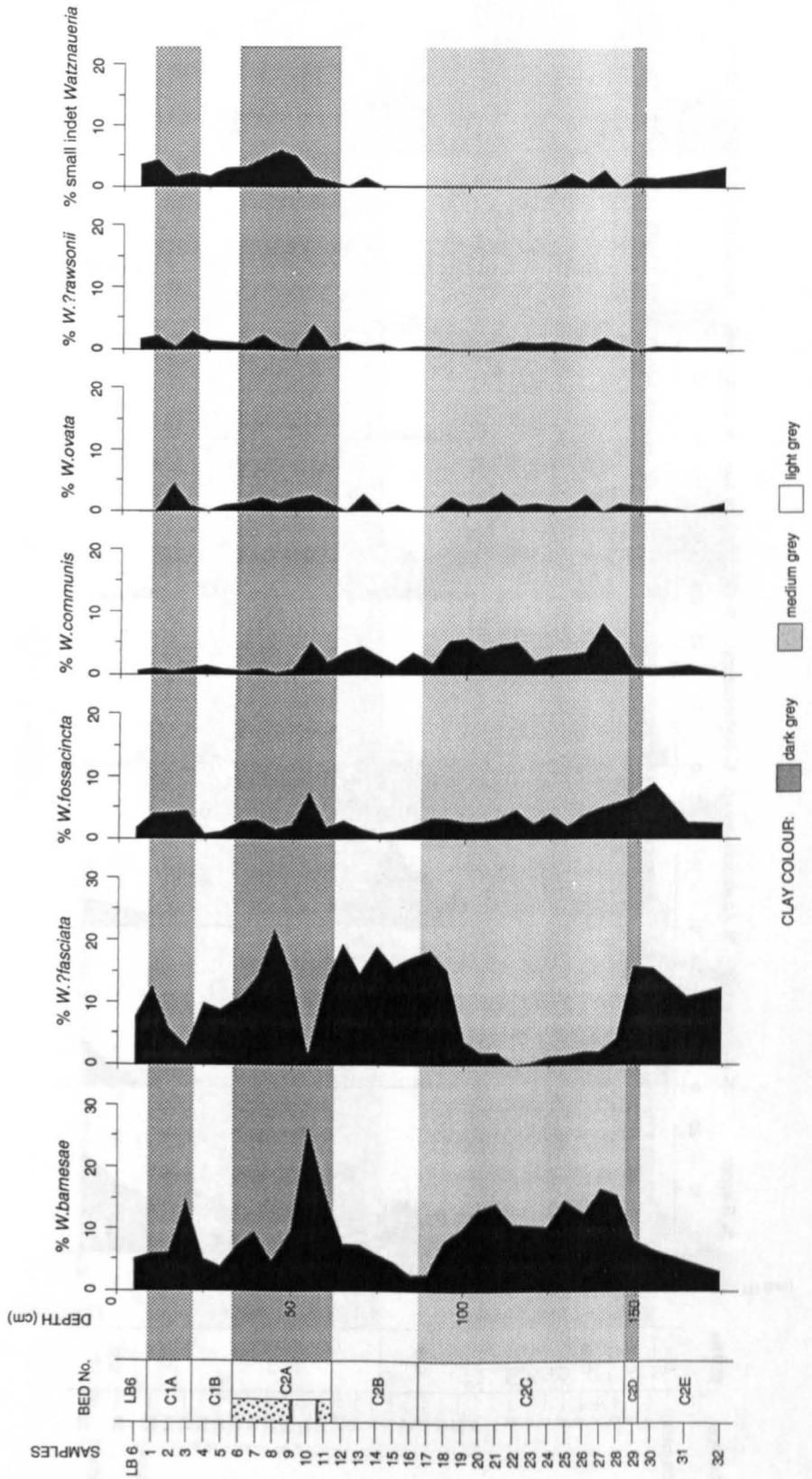


Fig. 4.7 - Relative abundance of the various species of *Watznaueria* through the pale/dark rhythmic section.

Darkening-upward cycle (Fig. 4.8)

Small-scale sedimentary cycles, involving upward darkening, are extensively developed in the Lower Barremian clays of Speeton (Rawson & Mutterlose, 1983). Each cycle is delimited by sharp pale/dark contacts; within the cycle the clay becomes progressively darker upward. This 1m thick section, across Bed LB1F of Speeton (*fissicostatum* Zone; Lower Barremian), spans a single darkening-upward cycle. This organic-rich part of the Speeton succession is correlatable with the Hauptbätterton unit of Germany, and the Munk Marl Bed of the central North Sea. The traditional interpretation of these cycles involves cyclical changes in atmospheric humidity - with increased humidity causing increased weathering of land areas, greater input of detrital material, and darkening of the clay. Overall nannofossil abundance is consistently rather low throughout this section (with only about 20 specimens per average field of view), but preservation appears consistently good, and the observed assemblage differences are believed to be primary, rather than diagenetically induced. Fig. 4.8 presents the distributions of major taxa through this section, and a tentative palaeoenvironmental interpretation.

Nannoconids are virtually absent in the pale, lower part of LB1F, but *N.abundans* becomes common to abundant higher in the cycle, and *N.borealis* "blooms" very dramatically towards the top of the bed. Nannoconids probably account for the bulk of the carbonate in sample LB1F (13) - a whole-rock SEM study of this sample revealed sediment surfaces covered in nannoconids (Plate 24). Thomsen (1989) observed almost monospecific coccolith assemblages, representing seasonal blooms, in the finely-laminated Munk Marl Bed of the central North Sea. The nannoconid bloom in the upper part of LB1F may have been just as brief, and dramatic (in terms of assemblage dominance), since the original species assemblages were probably affected by bioturbation in this not-so-finely laminated unit (in addition, the smear slide on which abundance figures are based represents a composite assemblage from many laminae). The peak abundance of *Nannoconus* in a dark, organic-rich horizon seems contrary to evidence from pale/dark rhythmically bedded sequences, in which nannoconids are most abundant in the paler, carbonate-rich horizons. This suggests that we are still a long way from fully understanding the environmental preferences of this enigmatic genus.

The "high fertility indices," *B.constans* and *Z.noeliae*, are most abundant in the pale, lower part of LB1F, and much depleted in the dark, upper part. *B.constans* increases in abundance earlier in the cycle than *Z.noeliae*; Erba (1992) observed a similar, longer-term pattern in the Pacific, and suggested that *B.constans* responded to increasing fertility earlier, at mesotrophic levels, than *Z.erectus* (= *Z.noeliae*). The distributions of these species are almost exactly opposite to that of *Nannoconus* - this would seem to support

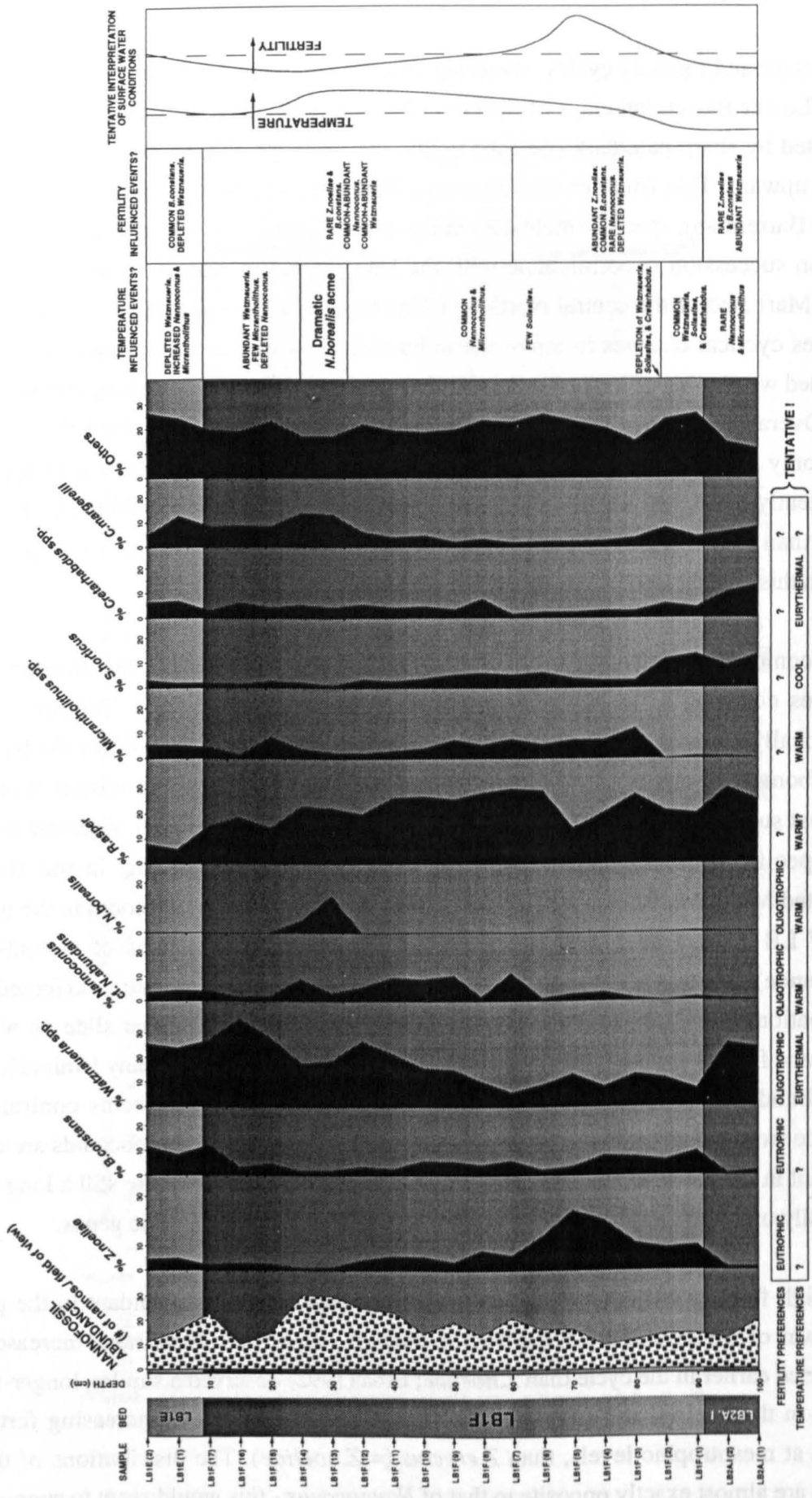


Fig. 4.8 - Distribution of main nannofossil taxa through a darkening-upward cycle, and a tentative interpretation of surface water conditions.

the recent conclusion of Coccioini *et al.* (*in press*), that nannoconids preferred oligotrophic conditions (low surface water fertility).

Sollasites horticus and *Micrantholithus* spp. also display interesting distributional trends, that might be temperature-related (Fig. 4.8). All this data could be variously interpreted in terms of temperature and fertility (e.g. Fig. 4.8) but, with the present state of knowledge, it is best to remain cautious. Even with 5cm spaced samples, significant, short-term acmes (= blooms) may have been missed. Further SEM examination of laminated horizons, lamina by lamina, should help deduce more precise palaeoenvironmental preferences.

C7/C8 faunal change interval (Fig. 4.9)

A major turnover of ammonite faunas, with replacement of Tethyan forms by Boreal forms, occurs across the C7/C8 boundary at Speeton (= the *regale-inversum* zonal boundary; late Early Hauterivian). Doyle (1989) described the lithology and ammonite faunas of these beds in great detail, and showed that the change-over from Tethyan to Boreal forms occurred in steps, with a rich suite of both Tethyan and Boreal ammonites in Bed C7H.II. These boundary beds were sampled at 5-10cm intervals (Fig. 4.9), to examine the response of nannoplankton to the changing palaeoceanographical conditions. However, nannofossil preservation is quite variable in this section, and the results are rather disappointing (Fig. 4.9) - no major assemblage differences are noticeable on this scale. In fact, if anything, the nannofossil assemblages seem to show an opposite trend to the ammonites - *C.salebrosum*, the only common species of well-documented cool-water affinity, is slightly more abundant below the boundary.

However, if we consider this interval in a wider, stratigraphical context then certain analogies become apparent. This interval corresponds approximately with the premature, regional extinctions of *Calcicalathina oblongata*, *Helenea quadrata*, and *Stradnerlithus silvaradius*, all of which are rare at Boreal latitudes and range considerably higher in Tethyan sections (Bergen, 1994). *Cruciellipsis cuvillieri*, another clearly Tethyan-derived species, that is nevertheless reasonably common in the Lower Hauterivian of the North Sea, is extremely rare above this level. This interval also coincides approximately with the disappearance of *Clepsilithus maculosus*; this species is absent from the mid-Hauterivian of North Sea sections, but reappeared in the Late Hauterivian. Furthermore, in the upper part of C7, only slightly above the closely-sampled interval, the cool-water species *C.salebrosum* increases dramatically in abundance; this "final flurry" (just prior to its mid-Hauterivian extinction) is also observed in Borehole 81/43. Thus, nannofossils tell a similar, if less dramatic story to ammonites.

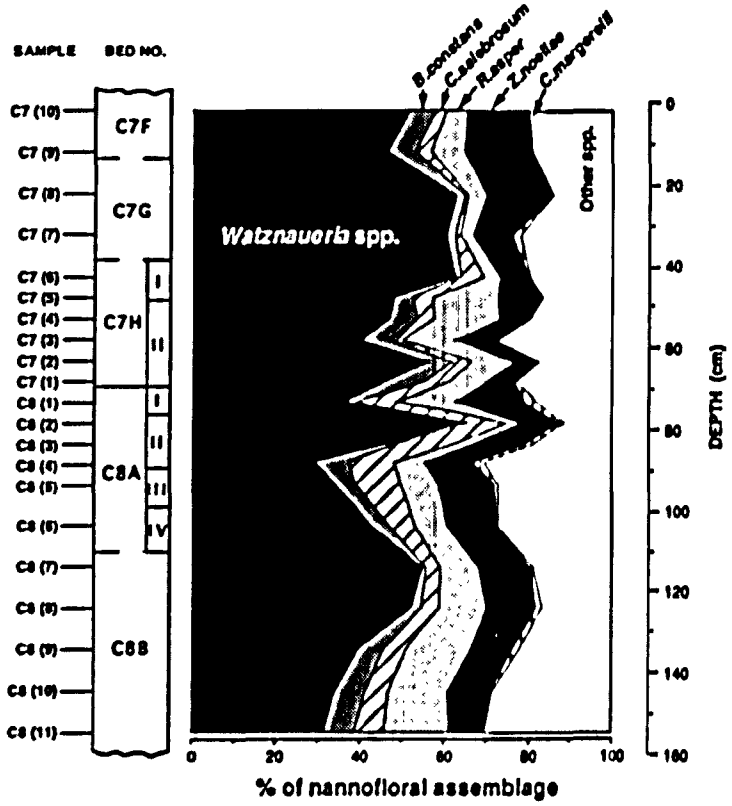


Fig. 4.9 - Nannofossil asemblage composition across the C7/C8 boundary section.

4.5 - NANNOPLANKTON MIGRATIONS DURING THE NEOCOMIAN

Crux (1989) and Mutterlose (1992b) have previously related patterns of nannoplankton migration to cephalopod migrations and sea-level changes, but a number of new observations can be made. These generally agree well with established sea-level curves (e.g. Rawson & Riley, 1982; Rawson, 1993) and cephalopod migrations (e.g. Kemper *et al.*, 1991; Rawson, 1993 and *in press*).

Late Ryazanian - Late Ryazanian assemblages of the North Sea and Barents Sea bear little resemblance to the Late Berriasian nannofloras of Tethys. The most characteristic species of this interval, *C.salebrosum*, *Kokia* spp., *Nannoconus* sp. (disk) and *S.arcuatus*, have not been recorded from Tethyan sections, and diverse Tethyan taxa are absent in Boreal sections. This undoubtedly reflects palaeogeographical isolation of these seaways, due to low sea-level stands.

Early Valanginian - The occurrence of abundant nannoconids in the earliest Valanginian of Core 7B, offshore mid-Norway, is suggestive of good marine

connections, to the west of Ireland, with the North Atlantic. The sudden *en mass* appearance of *Speetonia colligata* in Bed D3D at Speeton (lower *Polyptychites* spp. Zone), and at an equivalent level in Borehole 81/43, is indicative of transgression, and flooding of the North Sea basin by Tethyan sourced water. *S.colligata* originated in the latest Tithonian of Tethys (Bralower *et al.*, 1989), and is thus a late entrant to the Boreal area. *C.cuvillieri* also makes a belated first appearance during this interval. *A.jakubowskii* is extremely abundant during this transgressive interval. *M.speetonensis* and *T.shetlandensis*, previously thought to be restricted to the Boreal Realm, have recently been recorded in the Lower Valanginian *campylotoxum* Zone of S.E. France (Bergen, 1994, and *pers. obs.*). Thus, Boreal and Tethyan seaways seem to have been well connected during the late Early Valanginian. Despite these good connections, certain stenothermal Tethyan species (e.g. *C.oblongata*, *R.dekaenelii*, *T.verenae*) did not colonise the North Sea basin; this indicates the existence of a significant temperature gradient.

Late Valanginian - The limited Late Valanginian assemblages available are diverse, yielding many taxa present in Tethys. Tethyan nannoconids are quite common in the short early Late Valanginian-dated interval of Borehole 81/43. This suggests relatively good connections with Tethys. However, the more stenothermal Tethyan species (e.g. *C.oblongata*) are still absent.

Early Hauterivian - Early Hauterivian nannofloras of the North Sea area display a strong Tethyan influence - *C.oblongata*, one of the most stenothermal Tethyan species, entered the basin during this interval. Other Tethyan-derived species (e.g. *C.cuvillieri*, *H.quadrata*, *Nannoconus* spp., *Z.erectus*) are relatively common in this interval. *R.antiquus*, until recently thought to be restricted to the Boreal Realm, reached the North Atlantic and S.E. France (Bergen, 1994). These distributions suggest relatively high sea-levels, good marine connections, and a more equable climate.

'Mid' Hauterivian - A number of Tethyan taxa suffered premature regional extinction or rarefaction during the late Early Hauterivian; this suggests climatic cooling and/or closure of marine connections to the south. *C.maculosus* also withdrew from the area at this time, only to reappear in the late Late Hauterivian. The approximately synchronous first occurrences of four species (*P.plethotretus*, *P.tayloriae*, *R.windleyae* and *Z.scutula*) in the earliest Late Hauterivian are suggestive of transgression.

Late Hauterivian - Early Late Hauterivian nannofloras of the North Sea area lack a number of characteristic Tethyan elements (e.g. *C.cuvillieri*, *C.silvaradion*, *H.quadrata*, *L.bollii*). *T.septentrionalis*, the most characteristic element in Boreal sections, has not been extensively reported from Tethyan regions, but is known to be widely distributed

(e.g. Varol, 1992). *C.maculosus* is absent throughout the early Late Hauterivian, but re-entered the North Sea area during *gottschei* Zone times; this re-entry is associated with a sudden proliferation of *Micrantholithus* and *Z.noeliae*, and with the appearance of a particularly stenothermal Tethyan species, *L.bollii* (recorded in Core 7B and Borehole 81/43). These features, together with the resumption of sedimentation in Core 7B at this time, are very strongly suggestive of transgression, and relatively warm surface waters.

Barremian - The appearance of *A.terebrodentarius* in the *variabilis* Zone suggests that connections to Tethys were still open at this time. The rapid development of endemic taxa (*N.abundans* and *N.borealis*) and the disappearance of numerous species (e.g. *A.terebrodentarius*, *C.rothii*, *R.pseudoangustus*, *T.jurapelagicus*) suggest that basin isolation, caused by regression, occurred soon after - probably during *rarocinctum* Zone times. The diversity and abundance of endemic nannoconids in the restricted Boreal seaway suggest that this was a relatively warm period.

CONCLUSIONS

&

RECOMMENDATIONS

SUMMARY OF PRINCIPAL CONCLUSIONS

Taxonomy

- Nine new species, all recognisable on the light microscope, have been described. In addition, numerous light-microscopically distinct but indeterminate "spp." have been accurately characterised, and their ranges documented; further SEM work is required to ascertain the taxonomic status of these forms.
- It has been shown that several widely recognised forms have been consistently misidentified (e.g. *"D.lehmanii" = A.jakubowskii* sp. nov.; *"T.stradneri" = T.bergeni* sp. nov.; *"S.comptus" = C.maculosus* sp. nov.). Propagation of such misidentifications results in extended, composite ranges and reduced biostratigraphical potential.
- A relatively major, but conservative rationalisation of genera has been proposed, utilising existing genera as far as possible (two new genera - *Apertasphaera* and *Neoparhabdolithus* - have been erected to include particularly distinctive forms). A number of widely used genera have been shown to be invalid. The resultant, simplified generic classification should permit easier recognition of phylogenetic relationships; only when these are established can further subdivision of genera be warranted.
- Based on the generic rationalisation, an updated suprageneric classification has been constructed, and one new family (Family Tubodiscaceae) proposed. The suprageneric scheme is not, however, intended to be followed too rigidly; it serves as a useful means of categorising nannofossils, and should aid recognition of relationships.
- Consistent and precise taxonomy is the key to progression within nannopalaeontology - many biostratigraphical and palaeoceanographical anomalies can be attributed to taxonomic inconsistency.

Biostratigraphy

- Re-examination of the Speeton section, on which several nannofossil zonations have been based, has proven very worthwhile - closer sampling, refined species concepts, and greater analysis time have allowed identification of a number of datums, and many species, not recorded by previous authors.
- The nannofossil zonation presented herein is essentially a compilation of previous schemes (Jakubowski, 1987; Crux, 1989; Mutterlose, 1991), with the addition of some new datums. Refined taxonomy, closer sampling, and better sections (e.g. Borehole 81/43) have enabled integration of the various events utilised in previous zonations. The inconistencies between previous zonations can generally be traced to varying taxonomic concepts.
- The updated zonation scheme should enable dating of core samples with ammonite zonal precision, in the Upper Ryazanian-Barremian interval. Biostratigraphical

resolution within the Upper Hauterivian to Lower Barremian is considerably better than current ammonite zonations.

- This zonation, which is based on North Sea sections, can also be applied in the Barents Sea, although not all the markers utilised are proven to have ranged this far north.
- Comparison with new data from low-latitude sections has shown great potential for inter-regional correlation. A preliminary compilation of nannofossil datums shows that traditional, ammonite-based correlations are well-founded, but indicates that the Hauterivian-Barremian boundary may be placed slightly too low at Speeton.

Palaeoceanography

- Surface water temperature is believed to have been the primary factor controlling the distribution of Early Cretaceous nannoplankton - the palaeobiogeographical distributions of many species are clearly limited by palaeolatitude. As with living nannoplankton, stenothermal low-latitude forms are readily identified, but relatively few species show clear cool-water preferences. Within the Boreal Realm there was not a particularly dramatic northward decline in nannofloral diversity - Barents Sea and North Sea assemblages are essentially comparable.
- Several stenothermal Tethyan species, not previously recorded in Boreal sections, were observed in the present study (e.g. *Calcicalathina oblongata* and *Lithraphidites bollii*; the latter recorded as far north as offshore mid-Norway). Occasional influxes of these species seem to be correlatable across the North Sea basin, and probably record warm-water ingressions.
- Many species previously thought to be restricted to the Boreal Realm are present in Tethyan sections, and experience suggests that most remaining "endemic Boreal" forms will be shown to be widely distributed. *Crucibiscutum salebrosum* is the only Neocomian species to exhibit an indisputable cool-water preference; even if this species is recorded at low-latitudes, it could never attain the levels of abundance observed in Boreal areas.
- Nannoplankton provincialism was strong during the Late Ryazanian and Barremian, with clearly differentiated Boreal and Tethyan floras. However, provincialism was much less severe during the Valanginian-Hauterivian, and probably less intense than during many subsequent intervals.
- Diachroneities in the ranges of temperature-sensitive species (manifest by belated first occurrences, premature regional extinctions, and re-entries) may be useful in deducing changing palaeoclimatic and water-mass conditions.
- Previous palaeoceanographical studies have been hampered by broad species concepts, excessive lumping of recognised taxa, and insufficient biostratigraphical control. It is hardly surprising that only limited conclusions have been made.
- The use of certain poorly-defined taxa to deduce past conditions of surface water fertility is regarded with scepticism; modern nannoplankton are not very clearly limited

by fertility, and the evidence for such preferences among Cretaceous forms is unconvincing.

RECOMMENDATIONS & FUTURE WORK

- Original taxonomic descriptions should be consulted more often, and we should be wary of utilising taxa described from a very different stratigraphical level - many species are probably shorter-ranging than is commonly realised, and their quoted ranges are composite. Very poorly-defined taxa (e.g. *Chiastozygus litterarius*) are probably best discarded.
- Specimens should be illustrated at various degrees of tilt on the SEM - only by tilting can the full rim structure be discerned.
- LM-SEM transfer of the various "spp." recorded in this study should permit considerable taxonomic clarification (especially in the case of *Chiastozygus*). It is anticipated that most of these "spp." will be found to be undescribed.
- The zonation presented herein, while representing a considerable improvement on previous schemes, is regarded as preliminary. Increased sample coverage should enable much improved resolution; given sufficient material, the current level of resolution might easily be halved. The Upper Valanginian, Upper Barremian and the entire Aptian stage require further study. There is great potential for further subdivision of the Aptian, but this must await the availability of suitable (probably offshore) sections. Resolution within the Lower Hauterivian might be increased by closer examination of expanded German sections.
- Biostratigraphers should not feel tied to any "standard" zonation, no matter how well proven. A flexible, "bioevent" approach, utilising both discrete first and last occurrences and abundance data, is recommended. Even if a particular datum is proven to be strongly diachronous on an inter-regional scale, this does not preclude its use within a particular basin. The last occurrence datums and acme tops recognised in this study could be used to compile a zonation suitable for oil industrial purposes, while, for academic purposes, detailed examination of further core and outcrop material should enable integration of further datums within this framework.
- Future palaeoceanographical studies should exercise more stringent species concepts; complicated preparation techniques and/or extended counts are no substitute for a discerning eye. There is little point in conducting detailed statistical analyses of inherently flawed data sets. Isotopic techniques are unlikely to aid such interpretations, due to diagenetic modification of most Cretaceous sequences.
- On a geological time scale, the mere presence or absence of proven temperature-sensitive species within a section is more likely to be environmentally significant than abundance plots of major taxa. Such data can only be gathered by extended checking of slides, and by the application of improved biostratigraphical schemes. Once the pattern

of inter-regional migration has been established it should be easier to interpret the abundance fluctuations of major species.

REFERENCES

APPLEGATE, J.L. & BERGEN, J.A., 1989. Cretaceous calcareous nannofossil biostratigraphy of sediments recovered from the Galicia Margin, ODP Leg 103. P. 293-348 *in*: BOILLOT, A.C., WINTERER, E.L. *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, **103**.

APPLEGATE, J.L., BERGEN, J.A., COVINGTON, J.M. AND WISE, S.W., 1989. Lower Cretaceous calcareous nannofossils from continental margin drill sites off North Carolina (DSDP Leg 93) and Portugal (ODP Leg 103): a comparison. P. 212-222 *in* CRUX, J.A., & VAN HECK, S.E. (Eds.), *Nannofossils and their Applications*, British Micropalaeontological Society Series, Ellis Horwood Ltd., Chichester.

AARHUS, N., VERDENIUS, J. & BIRKELUND, T., 1986. Biostratigraphy of a Lower Cretaceous section from Sklinnabanken, Norway, with some comments on the Andøya exposure. *Norsk Geologisk Tidsskrift*, **66**, 17-43.

ÅRHUS, N., KELLY, S.R.A., COLLINS, J.S.H. & SANDY, M.R., 1990. Systematic palaeontology and biostratigraphy of two Early Cretaceous condensed sections from the Barents Sea. *Polar Research*, **8**, 165-194.

ÅRHUS, N., 1991. The transition from deposition of condensed carbonates to dark claystones in the Lower Cretaceous succession of the southwestern Barents Sea. *Norsk Geologisk Tiddsskrift*, **71**, 259-263.

BACKMAN, J. & SHACKLETON, N.J., 1983. Quantitative biochronology of Pliocene and early Pliestocene calcareous nannofossils from the Atlantic, Indian and Pacific oceans. *Marine Micropalaeontology*, **8**, 141-170.

BARRON, E.J., 1983. A warm, equable Cretaceous: the nature of the problem. *Earth Science Reviews*, **19**, 305-338.

BEAUFORT, L., 1991. Adaption of the random settling method for quantitative studies of calcareous nannofossils. *Micropalaeontology*, **37**(4), 415-418.

BERGEN, J.A., 1994. Berriasian to Early Aptian calcareous nannofossils from the Vocontian Trough (S.E. France) and deep sea drilling site 534: new nannofossil taxa and a summary of low-latitude biostratigraphic events. *Journal of Nannoplankton Research*, **16** (2), 59-69.

BLACK, M. & BARNES, B., 1959. The structure of Coccoliths from the English Chalk. *Geological Magazine*, **XCVI**, 311-333.

BLACK, M., 1971a. Coccoliths of the Speeton Clay and Sutterby Marl. *Proceedings of the Yorkshire Geological Society*, **38** (3), 381-424.

BLACK, M., 1971b. Problematical microfossils from the Gault Clay. *Geological Magazine*, **108**, 325-7.

BLACK, M., 1972. British Lower Cretaceous Coccoliths. I - Gault Clay (Part 1). *Palaeontological Society of London (Monograph)*, **126**, 1-48.

BLACK, M., 1973. British Lower Cretaceous Coccoliths. I - Gault Clay (Part 2). *Palaeontological Society of London (Monograph)*, **127**, 49-112.

BOUDREAUX, J.E. & HAY, W.W., 1969. Calcareous nannoplankton and biosratigraphy of the Late Pliocene-Pliestocene-Recent sediments of the submarex cores. *Rev. Esp. Micropaleontol.*, 1, 249-292.

BOWN, P.R., 1987a. The Stuctural Development of Early Mesozoic Coccoliths and its Evolutionary and Taxonomic Significance. *Abh. geol. Bundesanst.*, **39**, 33-49.

BOWN, P.R., 1987b. Taxonomy, evolution, and biostratigraphy of Late Triassic-Early Jurassic calcareous nannofossils. *Special Papers in Palaeontology*, **38**, 1-118.

BOWN, P.R., 1992. New calcareous nannofossil taxa from the Jurassic/Cretaceous boundary interval of Sites 765 and 261, Argos Abyssal Plain. P. 369-379 *in* GRADSTEIN, F.M., LUDDEN, J.N. *et al.*, 1992, *Proceedings of the Ocean Drilling Program, Scientific Results*, **123**.

BOWN, P.R., 1993. Early Cretaceous nannofossils from the eastern Indian Ocean: biostratigraphic and biogeographic observations. (Abstract) *INA Newsletter*, **15** (2), Salamanca abstracts volume.

BOWN, P.R., COOPER, M.K.E. & LORD, A.R., 1988. A Calcareous Nannofossil Biozonation Scheme for the early to mid Mesozoic. *Newsl. Stratigr.*, **20** (2), 91-114.

BOWN, P.R. & COOPER, M.K.E, 1989. New Calcareous Nannofossil taxa from the Jurassic. *Journal of Micropalaeontology*, **8** (1), 91-96.

BOWN, P.R. & OZKAN, S., 1992. Review of calcareous nannofossil biodtratigraphy and correlation across the Jurassic-Cretaceous boundary. *Memoire di Scienze Geologiche (Padova)*, **XLIII**, 77-87.

BRALOWER, T.J., 1987. Valanginian to Aptian calcareous nannofossil stratigraphy and correlation with the upper M-sequence magnetic anomalies. *Marine Micropalaeontology*, **11**, 293-310.

BRALOWER, T.J., 1989. Lower Cretaceous calcareous nannofossil stratigraphy of the Great Valley Sequence, Sacramento Valley, California. *Cretaceous Research*, **11**, 101-123.

BRALOWER, T.J., 1991. Lower Cretaceous calcareous nannofossil biostratigraphy of a North Sea borehole: implications for Boreal Cretaceous stratigraphy. *Proceedings of the Yorkshire Geological Society*, **48**, 421-434.

BRALOWER, T.J., MONECHI, S. & THIERSTEIN, H.R., 1989. Calcareous Nannofossil Zonation of the Jurassic-Cretaceous Boundary Interval and Correlation with the Geomagnetic Polarity Timescale. *Marine Micropalaeontology*, **14**, 153-235.

BRALOWER, T.J. & SIESSER, W.G., 1992. Cretaceous calcareous nannofossil biostratigraphy of Sites 761, 762, and 763, Exmouth and Wombat Plateaus, northwest Australia. P. 529-556 *in* VON RAD, U., HAQ, B.U.*et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, **122**.

BRÉHÉRET, J.G., 1983. Sur des niveaux de black shales dans l'Albien inferieur et moyen du domaine vocontien (sud-est de la France); etude de nannofacies et signification des palaeoenvironnement; essai d'interpretation genetique. *Bull. Mus. Natn. Hist. Paris*, ser.4, v.5 (C1), 113-159.

BÖNNIMANN, P., 1955. Microfossils *incertae sedis* from the Upper Jurassic and Lower Cretaceous of Cuba. *Micropalaeontology*, **1**, 28-51.

BUKRY, D., 1969. Upper Cretaceous coccoliths from Texas and Europe. *Univ. Kansas Paleontol. Contrib.*, **51** (Protista 2), 1-79.

BUSSON, G., & NOËL, D., 1991. Les nannoconidés, indicateurs environmentaux des océans et mers épicontinentales du Jurassique terminal et du Crétacé inférieur. *Oceanologica Acta*, **14** (4), 333-356.

CASEY, R., 1961. The stratigraphical palaeontology of the Lower Greensand. *Palaeontology*, **3** (4), 487-621.

CASEY, R. & RAWSON, P.F., 1973. A review of the boreal Lower Cretaceous. P.415-430 *in* CASEY, R. & RAWSON, P.F. (Eds.), *The Boreal Lower Cretaceous*, Geological Journal Special Issue No. 5, Seel House Press, Liverpool.

CEPEK, P. & HAY, W.W., 1969. Calcaroue nannoplankton and biostratigraphic subdivision of the Upper Cretaceous. *Trans. Gulf Coast Assoc. geol. Soc.*, **19**, 323-336.

COCCIONI, R., ERBA, E. & PREMOLI-SILVA, I., *in press*. Barremian - Aptian calcareous plankton biostratigraphy from the Gorgo Cerbara section (Marche, central Italy) and implications for plankton evolution.

COFFIN, M.F., GAHAGAN, L.M., LAWVER, L.A., LEE, T.-Y. & ROSENCRANTZ, E., 1992. Atlas of Mesozoic/Cenozoic reconstructions (200 Ma to Present Day), *PLATES Progress Report*, No. 1-0192, University of Texas Institute for Geophysics Technical Report No. 122, pp. 49.

COOPER, M.K.E., 1989. Nannofossil provincialism in the late Jurassic - Early Cretaceous (Kimmeridgian - Valanginian) Period. P. 223-246 *in* CRUX, J.A., and VAN HECK, S.E. (Eds), *Nannofossils and their Applications*. British Micropalaeontological Society Series, Ellis Horwood Ltd., Chichester.

COPE, J.C.W., INGHAM, J.K. & RAWSON, P.F., 1992. Atlas of Palaeogeography and Lithofacies. *The Geological Society Memoir*, **13.**

COVINGTON, J.M. & WISE, S.W., 1987. Calcareous nannofossil biostratigraphy of a Lower Cretaceous deep-sea fan complex: Deep Sea Drilling Project Leg 93 Site 603, lower continental rise off Cape Hatteras. P.617-660 *in* VAN HINTE, J.E., WISE, S.W. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, **93**, 617-660.

CRUX, J.A., 1986. *Tegulalithus* a new genus of Early Cretaceous calcareous nannofossils. *INA Newsletter*, **8**, 88-90.

CRUX, J.A., 1987. Six new species of calcareous nannofossils from the Lower Cretaceous strata of England and Germany. *INA Newsletter*, **9**, 30-35.

CRUX, J.A., 1989. Biostratigraphy and palaeogeographical applications of Lower Cretaceous nannofossils from north-western Europe. P. 143-211 *in* Crux, J.A., and van Heck, S.E. (Eds.), *Nannofossils and their Applications*. British Micropalaeontological Society Series, Ellis Horwood Ltd., Chichester.

CRUX, J.A., 1991. Albian calcareous nannofossils from the Gault Clay of Munday's Hill (Bedfordshire, England). *Journal of Micropalaeontology*, **10** (2), 203-222.

DAVEY, R.J., 1979. The stratigraphic distribution of dinocysts in the Portlandian (latest Jurassic) to Barremian (early Cretaceous) of northwest Europe. *American Association of Stratigraphic Palynologists Contributions Series*, **5B**, 49-81.

DEAN, W.E., 1994. The relationship between sea-level changes, facies changes and ammonite distributions in the Aptian-Albian of the Anglo-Paris basin. *Unpublished Ph.D. Thesis*, University College, London.

DEFLANDRE, G., 1947. *Braarudosphaera* nov. gen., type d'un famille nouvelle de Coccolithiphoidés actuels á éléments composites. *C. r. Seances Acad. Sci. Paris*, **225**, 439-470.

DEFLANDRE, G., 1959. Sur les nannofossiles calcaires et leur systématique. *Rev. Micropalaeontol.*, **2**, 127-152.

DEFLANDRE, G., 1963. Sur les Microrhabdulidés, famille nouvelle de nannofossiles calcaires. *C. r. Seances Acad. Sci. Paris*, **256**, 3484-6.

DEFLANDRE, G. & FERT, C., 1954. Observations sur les coccolithophoridés actuels et fossiles en microscopie ordinaire et électronique. *Annales de Paléontolgie*, **40**, 115-176.

DE KAENEL, E. & BERGEN, J.A., 1993. New Early and Middle Jurassic coccolith taxa and biostratigraphy from the eastern proto-Atlantic (Morocco, Portugal and DSDP Site 547 B). *Eclogae geol. Helv.*, **86** (3), 861-907.

DOYLE, J.C., 1989. The stratigraphy of a late Lower Hauterivian horizon in the Speeton Clay formation (Lower Cretaceous) of East Yorkshire. *Proceedings of the Geologists' Association*, **100**, 175-182.

DUXBURY, S. 1977. Palynostratigraphy of the Berriasian to Barremian of the Speeton Clay of speeton, England. *Palaeontographica Abteilung B*, **160**, 17-67.

DERES, F. & ACHÉRITEGUY, J., 1972. Contribution à l'étude des Nannoconidés dans le Crétacé inférieur du Bassin d'Aquitaine. *Mem. B.R.G.M., Fr.*, **77**.

DERES, F. & ACHÉRITEGUY, J., 1980. Biostratigraphie des Nannoconides. *Bulletin des Centre de Recherches Explororation-Production Elf-Aquitaine*, **4** (1), 1-53.

DITCHFIELD, P. & MARSHALL, J.D., 1989. Isotopic variation in rhythmically bedded chalks: palaeotemperature variation in the Upper Cretaceous. *Geology*, **17**, 842-845.

DUFOUR, T. & NOEL, D., 1970. Nannofossiles et constitution petrographique de la Majolica, des Schistes a Fucoides et de la Scaglia Rossa d'Ombrie (Italie). *Rev. Micropalaeont.*, **13** (2), 107-114.

EHRENDORFER, T. & AUBRY, M.-P., 1992. Calcareous nannoplankton changes across the Cretaceous/Palaeocene boundary in the southern Indian Ocean (Site 150) .P 451-470 *in* WISE, S.W., SCLICH, R., *et al.*, 1992. *Proceedings of the Ocean Drilling Program, Scientific Results*, **120**, 451-470.

ERBA, E., 1986. I Nannofollii calcarei nell' Aptiano-Albiano (Cretacico inferiore): biostratigraphia, palaeoceanographia e diagenesi degli Scista a Fucoidi del Pozzo Piobbico (Marche). *Unpublished Ph.D. Thesis*, Universita di Milano, 313 p..

ERBA, E., 1987. Mid-Cretaceous cyclic pelagic facies from the Umbrian-Marchean Basin: What do calcareous nannofossils suggest? *INA Newsletter*, **9**, 52-53.

ERBA, E., 1989. Upper Jurassic to Lower Cretaceous *Nannoconus* distribution in some sections from northern and central Italy. *Memoirie di Scienze Geologiche (Padova)*, **XLI**, 255-261.

ERBA, E., 1992. Middle Cretaceous calcareous nannofossils from the Western Pacific (ODP Leg 129): Evidence for palaeoequatorial crossings. In: LARSON, R.L., LANCELOT, Y. *et al.* (Editors), *Proceeding of the Ocean Drilling Program, Scientific Results*, **129**.

ERBA, E., CASTRADORI, D., & GUASTI, G., 1989. Calcareous nannofossils record fertility and temperature cycles: evidence from the Albian Gault Clay Formation. *INA Newsletter*, **11**, 57-58.

ERBA, E., CASTRADORI, D., & GUASTI, G. & RIPEPE, M., 1992. Calcareous nannofossils and Milankovitch cycles: the example of the Albian Gault Clay Formation (Southern England). *Palaeogeogeography, Palaeoclimatology, Palaeoecology*, **93**, 47-69.

FLETCHER, B.N., 1969. A lithological subdivision of the Speeton Clay C Beds (Hauterivian), East Yorkshire. *Proceedings of the Yorkshire Geological Society*, **37** (3), 323-327.

FLETCHER, B.N., 1973. The distribution of Lower Cretaceous (Berriasian-Barremian) foraminifera in the Speeton Clay. Pp.161-168 *in* CASEY, R. & RAWSON, P.F. (Eds.): *The Boreal Lower Cretaceous.* Geological Journal Special Issue No.5.

FORCHHEIMER, S., 1972. Scanning Electron Microscope studies of Cretaceous coccoliths from the Köpingsberg Borehole No.1, SE Sweden. *Sver. geol. Unders.*, ser. C 668, **65** (14), 1-141.

GALLAGHER, L.T., 1988. A technique for viewing the same nannofossil specimen in light microscope and scanning electron microscope using standard preparation materials. *Journal of Micropalaeontology*, **7** (1), 53-57.

GARD, G., 1987. Late Quaternary calcareous nannofossil biostratigraphy and sedimentation patterns: Fram Strait, Arctica. *Paleoceanography*, **2** (5), 519-529.

GARD, G., 1989. Variations in coccolith assemblages during the last glacial cycle in the high and mid-latitude Atlantic and Indian oceans. P. 108-121 *in* CRUX, J.A., and VAN HECK, S.E. (Eds.), *Nannofossils and their Applications.* British Micropalaeontological Society Series, Ellis Horwood Ltd., Chichester.

GARTNER, S., 1968. Coccoliths and related calcareous nannofossils from the Upper Cretaceous deposits of Texas and Arkansas. *Univ. Kansas Paleontol. Contrib.*, **48**, 1-56.

GALLOIS, R.W., 1975. A borehole section across the Barremian-Aptian boundary (Lower Cretaceous) at Skegness, Lincolnshire. *Proceedings of the Yorkshire Geological Society*, **40** (4), 499-503.

GRÜN, W. & ALLEMANN, F., 1975. The Lower Cretaceous of Caravaca (Spain): Berriasian Calcareous Nannoplankton of the Miravetes Section (Subbetic Zone, Prov. of Murcia). *Eclogae geol. Helv.*, **68** (1), 147-211.

GRÜN, W. & ZWEILI, F., 1980. Das kalkige Nannoplankton der Dogger-Malm-Grenze im Berner Jura bei Liesberg (Schweiz). *Jber. geol. Bundesanst*, **123** (1), 231-341.

HANCOCK, J.M., 1990. Chapter 9: Cretaceous. P. 255-272 *in* Glennie, K.W. (Ed.), *Introduction to the Petroleum Geology of the North Sea (3rd Edition).* Blackwell Scientific Publications.

HAQ. B.A., 1991. Sequence stratigraphy, sea-level change, and significance for the deep sea. P. 3-39 *in* MACDONALD, D.I.M. (Ed.), *Sedimentation, Tectonics and Eustasy - Sea-level Changes at Active Margins.* International Association of Sedimentologists, Special Publication No.12, Blackwell Scientific Publications.

HARLAND, W.B., ARMSTRONG, R.L., COX, A.V., CRAIG, L.E., SMITH, A.G., SMITH, D.G., 1989. *A geologic timescale.* Cambridge University Press.

HAY, W.W., 1977. Calcareous nannofossils. P. 1055-1200 *in* RAMSAY, A.T.S. (Ed.), *Oceanic Micropalaeontology.* Academic Press, London.

HILL, M.E., 1975. Selective dissolution of mid-Cretaceous (Cenomanian) calcareous nannofossils. *Micropalaeontology*, **21** (2), 227-235.

HILL, M.E., 1976. Lower Cretaceous calcareous nannofossils from Texas and Oklahoma. *Palaeontographica B*, **156**, 103-179.

HILL, M.E. & BRALOWER, T., 1987. Early Evolution, Stratigraphy and Taxonomy of *Eiffellithus eximius* and Closely-Related Species. *Abh. Geol. B.-A.*, **37**, 89-97.

HINE, N., 1990. Late Cenozoic calcareous nannoplankton from the northeast Atlantic. *Unpublished Ph.D. Thesis.*

HOEDEMAEKER, P.J. & BULOT, L.G. (reporters), 1990. Preliminary ammonite zonation for the Lower Cretaceous of the Mediterranean region: report. *Géologie Alpine*, **66**, 123-127.

HOEDEMAEKER, P.J. & COMPANY, M. (reporters), 1993. Ammonite zonation for the Lower Cretaceous of the Mediterranean region; basis for the stratigraphic correlation within I.G.C.P. Project 262. *Revta. Esp. Palaeont.*, **8**, 117-120.

JAKUBOWSKI, M., 1986. New calcareous nannofossil taxa from the Lower Cretaceous of the North Sea. *INA Newsletter*, **8**, 36-42.

JAKUBOWSKI, M., 1987. A proposed Lower Cretaceous calcareous nannofossil zonation scheme for the Moray Firth area of the North Sea. *Abhandlungen Geologischen Bundesanstalt*, **39**, 99-119.

JEREMIAH, J., *in press.* A proposed Albian nannofossil zonation for the United Kingdom and North Sea Basin. *Journal of Micropalaeontology.*

KAYE, P., 1964. Observations on the Speeton (Lower Cretaceous). *Geological Magazine*, **101** (4), 340-356.

KEMPER, E., 1961. Die Ammonitengattung *Platylenticeras* (=Garniera). *Beih. geol. JB.*, **47**, 1-195.

KEMPER, E., RAWSON, P.F. & THIEULOY, J.-P., 1981. Ammonites of Tethyan ancestry in the early Lower Cretaceous of north-west Europe. *Palaeontology*, **24** (2), 251-311.

KENT, D.V. & GRADSTEIN, F.M., 1985. A Cretaceous and Jurassic geochronology. *Geological Society of America Bulletin*, **96**, 1419-1427.

KEUPP, H. & MUTTERLOSE, J., 1984. Vertical distribution of Organisms in the D-Beds of Speeton (Lower Cretaceous, England) considering the Calcareous Dinoflagellate Cysts. *Facies*, **10**, 153-178.

KNOX, R.W. O'B, 1991. Ryazanian to Barremian mineral stratigraphy of the Speeton Clay in the UK southern North Sea Basin. *Proceedings of the Yorkshire Geological Society*, **48** (3), 255-264.

KOK, C.P., 1985. UFO 2; An Early Cretaceous nannofossil from the Central North Sea. *INA Newsletter*, **7**, 35, 38.

LAMBERT, B., 1986. The species notion within the genus *Braarudosphaera* Deflandre, 1947 - myth and reality. *Revue de Micropaléontologie*, **28** (4), 255-264.

LAMBERT, B., 1987. Nannofossiles calcaires de l'Albien supérieur et du Vraconnien du Cameroun méridional. *Cahiers de Micropaléontologie*, **2** (2), 33-91.

LAMPLUGH, G.W., 1889. On of the subdivisions of the Speeton Clay. *Quarterly Journal of the Geological Society of London*, **45**, 575-618.

LORD, A.R. & BOWN, P.R. (Eds.), 1987. *Mesozoic and Cenozoic Stratigraphical Micropalaeontology of the Dorset Coast and Isle of Wight, Southern England.* British Micropalaeontological Society, Field Guide No.1.

LOTT, G.K., FLETCHER, B.N. & WILKINSON, I.P., 1986. The stratigraphy of the Lower Cretaceous Speeton Clay Formationin a cored borehole off the coast of north-east England. *Proceedings of the Yorkshire Geological Society*, **46**, 39-56.

MANIVIT, H., 1971. Les nannofossiles calcaires du Crétacé français (de l'Aptien au Danien). Essai de biozonation appuyée sur les stratotypes. Thèse, Université de Paris.

MANIVIT, H., 1979. F. Les Nannofossiles (Hypostratotype Mesogéen de l'étage Valanginien). p.87-98 *in* Les Stratotypes Francais, **6**. Comite Français de Stratigraphie.

McINTYRE, A. & BÉ, A.W.H., 1967. Modern Coccolithophoridae of the Atlantic Ocean - 1. Placoliths and Cyrtoliths. *Deep-Sea Research*, **14**, 561-597.

MORTIMER, C.R., 1987. Upper Cretaceous Calcareous Nannofossil Biostratigraphy of the Southern Norwegian and Danish North Sea Area. *Abh. Geol. B.-A.*, **39**, 143-175.

MUTTERLOSE, J., 1984. Die Unterkreideeaufschlusse (Valangin-Alb) im Raum Hannover-Braunschweig. *Mitt. geol. Inst. Univ. Hannover*, **24**, 61 S.

MUTTERLOSE, J., 1987. Calcareous Nannofossils and Belemnites as warm-water indicators from the NW German Middle Aptian. *Geol. Jb.*, **96**, 293-313.

MUTTERLOSE, J., 1988. Das kalige nannoplankton des N.W. Deutschen Valangin und seine palaozeanographische deutung. *Berliner geowiss. Abh.*, **94**, 175-209.

MUTTERLOSE, J.,1989a. Temperature-controlled migration of calcareous nannofloras in the north-west European Aptian. P.122-144 *in* : CRUX, J.A., and VAN HECK, S.E. (Eds.), *Nannofossils and their Applications*. British Micropalaeontological Society Series, Ellis Horwood Ltd., Chichester.

MUTTERLOSE, J., 1989b. Faunal and floral distribution in late Hauterivian rhythmic bedded sequences and their implications. *In* WIEDMANN, J. (Ed.), *Cretaceous of the Western Tethys*, Proceedings of the Third International Cretaceous Symposium.

MUTTERLOSE, J., 1991a. Das Verteilungs- und Migrationsmuster des kalkigen Nannoplanktons in der borealen Unterkreide (Valangin-Apt) NW-Deutschlands. *Palaeontographica*, **B 221**, 27-152.

MUTTERLOSE, J., 1991b. Die sedimentaren Rhythmen der Unterkreide NW-Deutschlands. *DGMK Berichte*, **468**, 373-388.

MUTTERLOSE, J., 1992a. Lower Cretaceous nannofossil biostratigraphy off northwestern Australia (Leg 123). P.343-368 *in* GRADSTEIN, F.M., LUDDEN, J.N., *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, **123**.

MUTTERLOSE, J., 1992b. Migration and evolution patterns of floras and faunas in marine Early Cretaceous sediments of N.W. Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **94**, 261-282.

MUTTERLOSE, J., 1992c. Biostratigraphy and palaeobiogeography of Early Cretaceous calcareous nannofossils. *Cretaceous Research*, **13**, 167-189.

MUTTERLOSE, J., & HARDING, I., 1987. Phytoplankton from the anoxic sediments of the Barremian (Lower Cretaceous) of north-west Germany. *Abh. Geol. B.-A.*, **39**, 177-215.

MUTTERLOSE, J., PINCKNEY, G. & RAWSON, P.F., 1987. The belemnite *Acroteuthis* in the *Hibolites* Beds (Hauterivian-Barremian) of North-West Europe. *Palaeontology*, **30** (3), 635-645.

MUTTERLOSE, J. & WISE, S.W., 1990. Lower Cretaceous nannofossil biostratigraphy of ODP Leg 113 Holes 692B and 693A, continental slope off east Antarctica, Weddell Sea. P.325-351 *in* BARKER, P.F., KENNET, J.P. *et al.*, *Proceedings of the Ocean Drilling Program, Scientific Results*, **113**.

NEALE, J.W., 1960. The Subdivision of the Upper D Beds of the Speeton Clay of Speeton, East Yorkshire. *Geological Magazine*, **XCVII**, 353-362.

NEALE, J.W., 1962. Ammonoidea from the lower D Beds (Berriasian) of the Speeton Clay. *Palaeontology*, **5** (2), 272-296.

NEALE, J.W., 1971. Microfaunas and some aspects of the Speeton Clay environment. P. 663-681 *in* OERTLI, H.J. (Ed.): *Colloquium on the palaeoecology of ostracodes.* Bulletin du Centre du Recherches de Pau - SNPA No.5 (Supplement).

NEALE, J.W., 1978. The Cretaceous. P. 325-384 *in* BATE, R. & ROBINSON, E. (Eds.): *A stratigraphical index of the British Ostracoda.* Geological Journal Special Issue No.8.

NOËL, D., 1965. Note préliminaire sur des Coccolithes jurassiques. *Cahiers de Micropaléontologie*, **1** (1), 1-25.

NOËL, D., 1968. Nature et genese des alternances de marnes et de calcaires du Barremien superieur d'Angle (Fosse Vocontienne, Basses Alpes). *C.R. Acad. Sci. Paris*, **266**, 1223-1225.

NOËL, D. & MANIVIT, H., 1978. Nannofacies de "black shales" apteinnes et albiennes d'Atlantique sud (legs 36 et 40). Interet sedimentologique. *Bull. Soc. Geol. France*, **7**, 491-502.

NOËL, D. & MELGUEN, M., 1978. Nannofacies of Cape Basin and Walvis Ridge sediments. Lower Cretaceous to Pliocene (Leg 40). P. 487-524 *in* BOLLI, H.M., RYAN, W.B.F. *et al.*, *Init. Repts. DSDP*, **40**, Washington (U.S. Govt. Printing Office), 487-524.

NORRIS, R.E., 1965. Living cells of *Ceratolithus cristatus* (Coccolithophorineae). *Arch. Protistenck. Bd.*, **108**, 19-24.

OKADA, H. & HONJO, S., 1973. The distribution of oceanic coccolithophorids in the Pacific. *Deep-Sea Research*, **20**, 355-374.

OWEN, H.G., 1971. Middle Albian Stratigraphy in the Anglo-Paris Basin. *Bulletin of the British Museum (Natural History)*, Supplement 8, London.

PARRISH, J.T. & CURTIS, R., 1982. Atmospheric circulation, upwelling, and organic-rich rocks in the Mesozoic and Cenozoic Eras. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **40**, 31-66.

PEDERSON, T.F. & CALVERT, S.E., 1990. Anoxia vs. Productivity: What Controls the Formation of Organic-Rich Sediments and Sedimentary Rocks? *The American Association of Petroleum Geologists Bulletin*, **74** (4), 454-466.

PERCH-NIELSEN, K., 1979. Calcareous Nannofossils from the Cretaceous between the North Sea and the Mediterranean. In *Aspekte der Kreide Europas. IUGS Series A*, **6**, 223-272.

PERCH-NIELSEN, K., 1985. Mesozoic calcareous nannofossils. P. 329-426 *in* BOLLI *et al.* (Eds.), *Plankton Stratigraphy*, Cambridge University Press.

PERCH-NIELSEN, K., 1985. Cenozoic calcareous nannofossils. P.427-554 *in* BOLLI *et al.* (Eds.), *Plankton Stratigraphy*, Cambridge University Press.

PERCH-NIELSEN, K., 1988. New Lower Cretaceous calcareous nannofossil species from England. *INA Newsletter*, **10**, 30-37.

PREMOLI SILVA, I., ERBA, E., & TORNAGHI, M.E., 1989. Palaeoenvironmental signals and changes in surface fertility in Mid Cretaceous C-org-rich pelagic facies of the Fucoid Marls (central Italy). *Geobios.*, mémoire spécial no. 11, 225-236.

RAWSON, P., 1971. The Hauterivian (Lower Cretaceous) biostratigraphy of the Speeton Clay of Yorkshire, England. *Newsletters in Stratigraphy*, **1**, 61-75.

RAWSON, P.F., 1973. Lower Cretaceous (Ryazanian-Barremian) marine connections and cephalopod migrations between the Tethyan and Boreal Realms. P. 131-144 *in* CASEY, R. & RAWSON, P.F. (Eds.), *The Boreal Lower Cretaceous.* Geological Journal Special Issue No.5, Seel House Press, Liverpool.

RAWSON, P.F., 1983. The Valanginian to Aptian stages - current definitions and outstanding problems. *Zitteliana*, **10**, 493-500.

RAWSON, P.F., 1992. Biogeographical affinities of N.W. European Barremian ammonite faunas and their palaeogeographical implications. (Abstract) *Fourth International Cretaceous Symposium (Hamburg), Abstracts Volume.*

RAWSON, P.F., 1993. The influence of sea-level changes on the migration and evolution of early Cretaceous (pre-Aptian) ammonites. P.227-242 *in* HOUSE, M.R. (Ed.), *The Ammonoidea: Environment, Ecology, and Evolutionary Change.* Systematics Association Special Volume No. **47**, Clarendon Press, Oxford.

RAWSON, P.F., *in press.* Sea level changes and their influence on ammonite biogeography in the European Lower Cretaceous. *Atti del 3 convegno internationale, fossili, evoluzione, ambiente, Pergola 1990.*

RAWSON, P.F., CURRY, D., DILLEY, F.C., HANCOCK, J.M., KENNEDY, W.J., NEALE, J.W., WOOD, C.J., WORSSAM, B.C., 1978. *A correlation of Cretaceous rocks in the British Isles.* Geological Society of London Special Report, **9**, 1-70.

RAWSON, P.F. & MUTTERLOSE, J., 1983. Stratigraphy of the Lower B and basal Cement Beds (Barremian) of the Speeton Clay, Yorkshire, England. *Proceedings of the Geologists' Association*, **94**, 133-146.

RAWSON, P.F. & RILEY, L.A., 1982. Latest Jurassic - Early Cretaceous Events and the "Late Cimmerian Unconformity" in the North Sea Area. *The American Association of Petroleum Geologists Bulletin*, **66**, 2628-2648.

REID, R.E.H., 1973. Origin of the Mesozoic 'Boreal' realm (correspondence). *Geological Magazine*, **110** (1), 67-69.

REINHARDT, P., 1965. Neue Familien für fossile Kalkflagellaten (Coccolithophoriden, Coccolithineen). *Monatsber. Dt. Akad. Wiss. Berlin*, **7**, 30-40.

RHYS, G.H., 1974. A proposed standard lithostratigraphic nomenclature for the southern North Sea: and an outline structural nomenclature for the whole of the (UK) North Sea. *Inst. Geol. Sci. Rept.*, **74/8**.

ROOD, A.P., HAY, W.W. & BARNARD, T., 1971. Electron Microscope studies of Oxford Clay coccoliths. *Eclog. geol. Helv.*, **64** (2), 245-272.

ROOD, A.P., HAY, W.W. & BARNARD, T., 1973. Electron Microscope studies of Lower and Middle Jurassic coccoliths. *Eclog. geol. Helv.*, **66** (2), 365-382.

ROTH, P.H., 1973. Calcareous nannofossils - Leg 17, DSDP. *Initial Reports of the Deep Sea Drilling Project*, **17**, 695-793.

ROTH, P.H., 1978. Cretaceous nannoplankton biostratigraphy and oceanography of the northwestern Atlantic ocean. P.731-759 *in* BENSON, W.E., SHERIDAN, R.E. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, **44**, U.S. Government Printing Office, Washington D.C..

ROTH, P.H., 1981. Mid-Cretaceous calcareous nannoplankton from the central Pacific: implications for palaeoceanography. P. 471-489 *in* THIEDE, J., VALLIER, T.L. *et al.*, *Init. Rept. DSDP*, **62**: U.S. Government Printing Office, Washington D.C..

ROTH, P.H., 1983. Jurassic and Lower Cretaceous calcareous nannofossils in the western North Atlantic (Site 534): biostratigraphy, preservation, and some observations on biogeography and palaeoceanography. P.587-621 *in* SHERIDAN, R.E., GRADSTEIN, F.M. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, **76**: U.S. Government Printing Office, Washington D.C..

ROTH, P.H. & BOWDLER, J.L., 1981. Middle Cretaceous calcareous nannoplankton biogeographpy and oceanography of the Atlantic ocean. *Society of Economic Palaeontologists and Mineralogists, Special Publication*, No. 32, 517-546.

ROTH, P.H. & KRUMBACH, K.R., 1986. Middle Cretaceous calcareous nannofossil biogeography and preservation in the Atlantic and Indian oceans: implications for palaeoceanography. *Marine Micropalaeontology*, **10**, 235-266.

ROTH, P.H. & THIERSTEIN, H., 1972. Calcareous nannoplankton: Leg 14 of the Deep Sea Drilling Project. P.421-485 *in* HAYES, D.E., PIMM, A.C. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, **14**. U.S. Government Printing Service, Washington D.C..

RUFFELL, A.H. & BATTEN, D.J., 1990. The Barremian-Aptian arid phase in western Europe. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **80**, 197-212.

SIMPSON, M.I., 1985. The stratigraphy of the Atherfield Clay Formation (Lower Aptian, Lower Cretaceous) at the type and other localities in southern England. *Proceedings of the Geologists' Association*, **96**, 23-44.

SISSINGH, W., 1977. Biostratigraphy of Cretaceous calcareous nannoplankton. *Geol. Mijnbouw.*, **56** (1), 37-65.

STRADNER, H., ADAMIKER, D. & PAPP, A., 1968. Electron Microscope studies on Albian calcareous nannoplankton from the Delft 2 and Leidschendam 1 Deep wells, Holland. *Verh. Kon. Ned. Akad. Wetensch., Afd. Natuurk.*, I., **24** (4), 1-107.

STRADNER, H. & GRÜN, W., 1973. On *Nannoconus abundans* nov. spec. and on Laminated Calcite Growth in Lower Cretaceous Nannofossils. *Verh. Geol. B.-A.*, **2**, 267-283.

SWINNERTON, H.H., 1935. The rocks below the Red Chalk of Lincolnshire, and their cephalopod faunas. *Q. Jl. geol. Soc. Lond.*, **91**, 1-46.

TAYLOR, R.J., 1978. The distribution of calcareous nannofossils in the Speeton Clay (Lower Cretaceous) of Yorkshire. *Proceedings of the Yorkshire Geological Society*, **42** (2), 195-209.

TAYLOR, R.J., 1982. Lower Cretaceous (Ryazanian to Albian) calcareous nannofossils. P.40-80 *in* LORD, A.R. (Ed.), *A Stratigraphical Index of Calcareous Nannofossils*, Ellis Horwood, Chichester.

THIERSTEIN, H.R., 1971. Tentative Lower Cretaceous Calcareous Nannoplankton Zonation. *Ecologae geol. Helv.*, **64** (3), 459-488.

THIERSTEIN, H.R., 1973. Lower Cretaceous calcareous nannoplankton biostratigraphy. *Abhandlungen Geologischen Bundesanstalt*, **29**, 1-52.

THIERSTEIN, H.R., 1976. Mesozoic calcareous nannoplankton biostatigraphy of marine sediments. *Marine Micropalaeontoly*, **1**, 325-362.

THIERSTEIN, H.R., 1980. Selective dissolution of Late Cretaceous and Earliest Tertiary calcareous nannofossils: experimental evidence. *Cretaceous Research*, **2**, 165-176.

THIERSTEIN, H.R., 1981. Late Cretaceous nannoplankton and the change at the Cretaceous-Tertiary boundary. *Society of Economic Palaeontologists and Mineralogists, Special Publication*, No.32, 355-394.

THIERSTEIN, H.R., GEITZENAUER, K.R., MOLFINO, B. & SHACKLETON, N.J., 1977. Global synchroneity of late Quaternary coccolith datum levels: Validation by oxygen isotopes. *Geology*, **5**, 400-404.

THIERSTEIN, H.R. AND ROTH, P.H., 1991. Stable isotopic and carbonate cyclicity in Lower Cretaceous deep-sea sediments: Dominance of diagenetic effects. *Marine Geology*, **97**, 1-34.

THOMSEN, E., 1987. Lower Cretaceous calcareous nannofossil biostratigraphy in the Danish Central Trough. *Danmarks Geologiske Undersøgelse*, Series A, **20**, 1-89.

THOMSEN, E., 1989. Seasonal variability in the production of Lower Cretaceous calcareous nannoplankton. *Geology*, **17**, 715-717.

TREJO, M., 1959. Dos nuevas especies del Genero *Nannoconus. Ciencia*, **19**, 130-132.

TREJO, M., 1960. La Famila Nannoconidae y su alcance estratographico en America (Protozoa, *incertae saedis*). Boletin de la Asociacion Mexicana de Geólogos Petroleros, **12**, 259-314.

TYSON, R.V. & FUNNELL, B.M., 1987. European Cretaceous shorelines, stage by stage. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **59**, 69-91.

VAN NIEL, B.E., 1992. New observations on the morphology of *Nannoconus*. *Znihovnicka ZPN*, **14a**, vol.1, p.73-85.

VAN NIEL, B.E., 1994. Scanning electron micrographs of the genus *Kokia* (*incertae sedis*). *Journal of Nannoplankton Research*, **16** (2), 75-77.

VAROL, O., 1989. Palaeocene calcareous nannofossil biostratigraphy. P. 267-310 *in* Crux, J.A., and van Heck, S.E. (Eds.), *Nannofossils and their Applications*. British Micropalaeontological Society Series, Ellis Horwood Ltd., Chichester.

VAROL, O., 1991. New Cretaceous and Tertiary Calcareous Nannofossils. *N. Jb. Geol. Paläont. Abh.*, **182** (2), 211-237.

VAROL, O., 1992. Taxonomic revision of the Polyclolithaceae and its contribution to Cretaceous biostratigraphy. *Newsletters of Stratigraphy*, **27** (3), 93-127.

VAROL, O. & GIRGIS, M.H., 1994. New taxa and taxonomy of some Jurassic to Cretaceous calcareous nannofossils. *N. Jb. Geol. Paläont. Abh.*, **192** (1), 153-185.

VAROL, O. & HOUGHTON, S.D., 1993. A review and classification of fossil didemnid ascidian spicules from fine-grained sediments. *INA Newsletter*, **15** (2), 98-99 (Salamanca Abstracts Volume).

VAROL, O. & HOUGHTON, S.D., *in press*. A review and classification of fossil didemnid ascidian spicules from fine-grained sediments. *Journal of Micropalaeontology*.

VERDENIUS, J.G., 1978. A Valanginian calcareous nannofossil association from Kong Karls Land, Eastern Svalbard. *Norsk Polarinstitutt, Notiser*, 350-352.

WATKINS, D.K., 1989. Nannoplankton productivity fluctuations and rhythmically bedded pelagic carbonates of the Greenhorn Limestone (Upper Cretaceous). *Palaeogeography, Palaeoclimatology, Palaeoecology*, **74**, 75-86.

WATKINS, D.K. & BOWDLER, J.L., 1984. Cretaceous calcareous nannofossils from Deep Sea Drilling Project Leg 77, southeast Gulf of Mexico. P.649-674 *in* BUFFER, R.T., SCHLAGER, W. *et al.*, *Initial Reports of the Deep Sea Drilling Project*, **77**, U.S. Government Printing Office, Washington D.C..

WEAVER, P.P.E. & HINE, N., *in press*. Calcareous nannofossils from the Quaternary of the north-east Atlantic Ocean. In: LORD, A.R. (Ed.), Stratigraphic index of calcareous nannofossils. British Micropalaeontological Society Special Publication.

WEAVER, P.P.E. & PUJOL, C., 1988. History of the last deglaciation in the Alboran Sea (Western Mediterranean) and adjacent North Atlantic as revealed by coccolith floras. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **64**, 35-42.

WEI, W., 1988. A new technique for preparing quantitative nannofossil slides. *Journal of Palaeontology*, **62**(3), 472-473.

WILLIAMS, J.R. & BRALOWER, T.J., *manuscript*. Nannofossil assemblages, fine fraction isotopes and the paleoceanography of the Early Cretaceous North Sea Basin.

WIND, F.H. & CEPEK, P., 1979. Lower Cretaceous calcareous nannoplankton from DSDP Hole 397A (northwest African Margin). P.221-235 *in* VON RAD, U., RYAN, W.B.F. *et al., Initial Reports of the Deep Sea Drilling Project*, **47** (A). U.S. Government Printing Service, Washington D.C..

WINTER, A., JORDAN, R.C. & ROTH, P.H., 1994. Biogeography of living coccolithophores in ocean waters. P. 161-177 *in* WINTER, A. & SIESSER, W.G. (Editors). *Coccolithophores*. Cambridge University Press, 242 pp..

WISE, S.W., Jr., 1983. Mesozoic and Cenozoic calcareous nannofossils recovered by Deep Sea Drilling Project Leg 71 in the Falkland Plateau region, southwest Atlantic Ocean. *Initial Reports of the Deep Sea Drilling Project*, **71**, p.481-550. U.S. Government Printing Office, Washington D.C..

WISE, S.W., 1988. Mesozoic-Cenozoic history of calcareous nannofossils in the region of the southern ocean. *Palaeogeography, Palaeoclimatology, Palaeoecology*, **67**, 157-179.

WISE, S.W. & WIND, F.H., 1977. Mesozoic and Cenozoic calcareous nannofossils recovered by DSDP Leg 36 drilling on the Falkland Plateau, south-west Atlantic sector of the Southern Ocean. P. 269-491 *in* BARKER, P.F., DALZIEL, I.W.D. *et al.., Init. Rept. DSDP*, **36**. U.S. Government Printing Office, Washington D.C..

WORSLEY, T.R., 1971. Calcareous nannofossil zonation of Upper Jurassic and Lower Cretaceous sediments from the Western Atlantic. *Proceedings of the Second Planktonic Conference (Roma, 1970)*, 1301-1321.

YOUNG, J.R. & BOWN, P.R., 1991. An ontogenetic sequence of coccoliths from the Late Jurassic Kimmmeridge Clay of England. *Palaeontology*, **34** (4), 843-850.

YOUNG, J.R., DIDYMUS, J.M., BOWN, P.R., PRINS, B. & MANN, S., 1992. Crystal assembly and phlogenetic evolution in heterococcoliths. *Nature*, **356**, 516-518.

ZIEGLER, P.A., 1975. North Sea Basin History in the Tectonic Framework of North-Western Europe. P.131-147 *in* WOODLAND, A.W. (Ed.), *Petroleum & the continental shelf of north-west Europe* (Vol.1).

APPENDIX

(RANGE CHARTS)

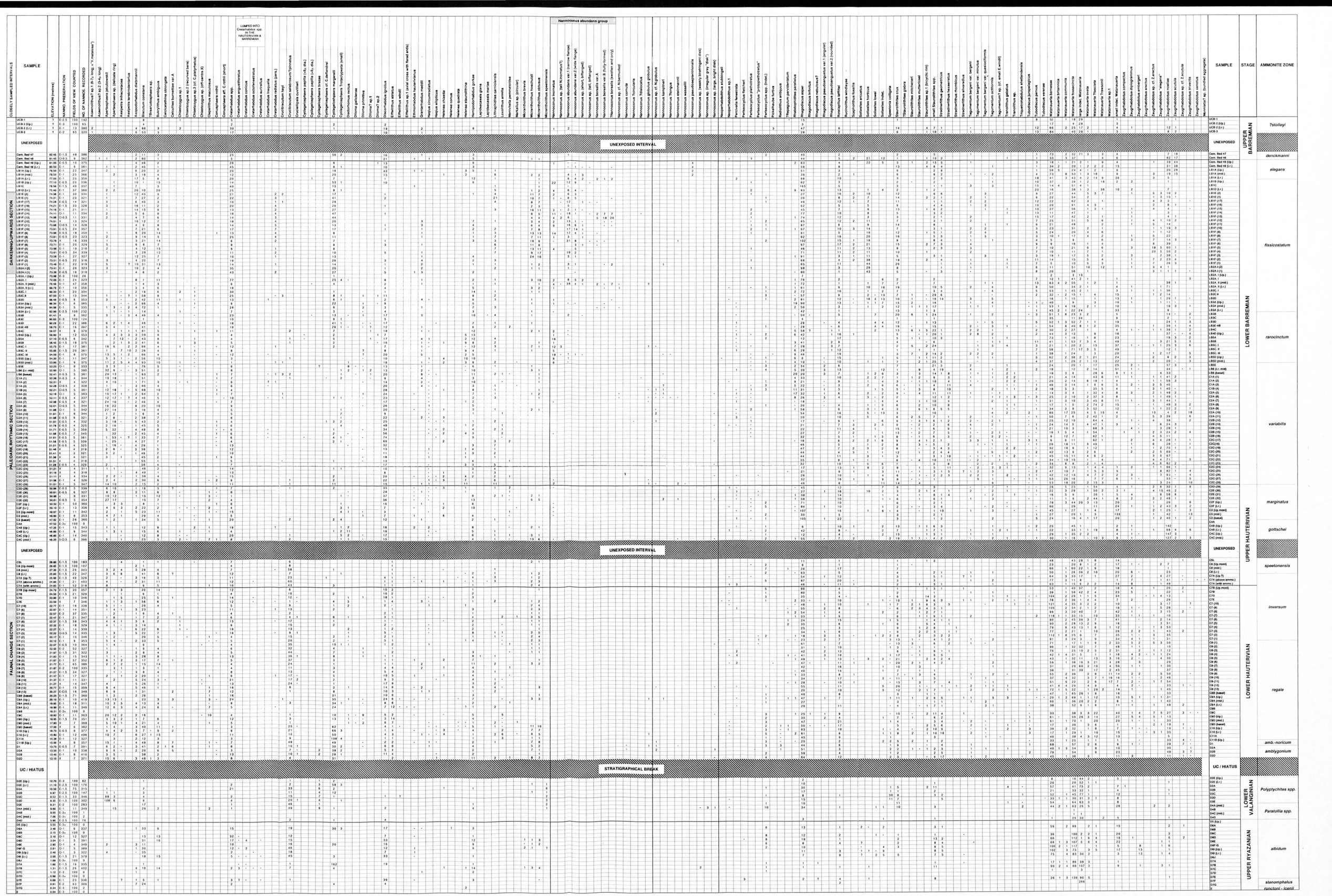
The back cover pocket contains charts displaying the stratigraphical distribution of calcareous nannofossils in the following sections:

Chart 1 - Speeton
Chart 2 - German outcrop material (composite section)
Chart 3 - Borehole 81/43
Chart 4 - Core 7B
Chart 5 - Core 7425/9-U-1
Chart 6 - Core 7430/10-U-1
Chart 7 - Atherfield Clay
Chart 8 - Skegness Borehole
Chart 9 - Heslerton Borehole

The following **counting procedure** was applied (see sections 1.6 & 1.7): at least 300 specimens, or a maximum of 100 fields of view (at 1,250x magnification), were counted in each slide; spots (•) indicate additional ocurrences, recorded outside the standard count.

Nannofossil preservation was estimated using the following scale (see section 1.8): E-1 to E-3 indicate increased degrees of etching; O-1 to O-3 indicate increasing overgrowth; X indicates excellent preservation.

Taxa are arranged alphabetically, to facilitate location.


CLOSELY SAMPLED INTERVALS
SAMPLE
ELEVATION (metres)
NANNO. PRESERVATION
FIELDS OF VIEW COUNTED
NO. OF NANNOS. RECORDED
Acaenolithus? sp. (Jeng, c.*V.marsalae*)
Acaenolithus? sp.1 (R-7); (orig., c.*V.marsalae*)
Aspidilithus? sp. (*A.ewingii*)
Aspidilithus? sp. (*A.fimbriatus*)
Aspidilithus? sp. (*A.fimbriatus* group)
Aspidilithus? sp. (*A.fimbriatus* s.l.)
Aspidilithus? sp. (*A.fimbriatus* s.s.)
Aspidilithus? sp. (*A.fimbriatus* s.s. with flared ends)
Aspidilithus? sp. (*A.fimbriatus* s.s. with pointed ends)
Aspidilithus? sp. (*A.fimbriatus* s.s. with rounded ends)
Aspidilithus? sp. (*A.fimbriatus* s.s. with unequal ends)
Aspidilithus? sp. (*A.fimbriatus* s.s. with unequal ends and only

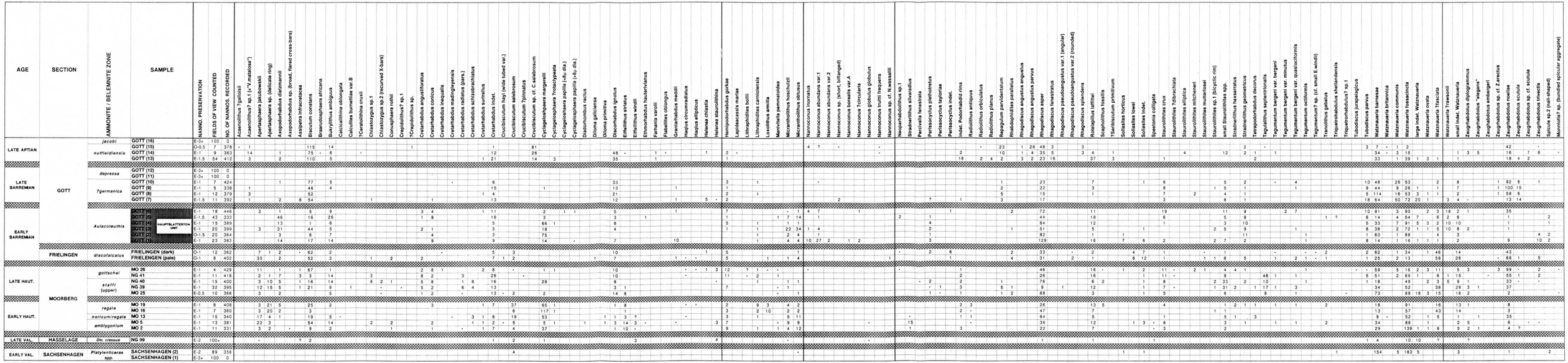


Chart 2 - German Outcrop Material

Stratigraphical distribution of calcareous nannofossils. Hatched areas represent sizeable sampling gaps.

| SAMPLE | DEPTH (metres) | NANNO. PRESERVATION | YIELDS OF VIEW COUNTED | NO. OF NANNOS. RECORDED | *Tubodiscoaster? tipo 2 (24-ray ring)* | *Asperbasilaqua jakubowskii* | *Asperbasilaqua sp. (delicate ring)* | *Axopodorhabdus dietzmannii* | *Assipetra infracretacea* | *Assipetra lombrodontarius* | *Assipetra sp.1 (circular)* | *Blaculcum constans* | *Bukrylithus ambiguus* | *Calculites bumettiae* var.A (=*Calculites? sp.1*) | *Calculites bumettiae* var.B (unornamented) | *Calculites bumettiae* var.C | *Chiastozygus sp.1* | *Chiastozygus sp.2* (recurved bars) | *Chiastozygus sp.3* (cf. *C.platymetus*) | *Chiastozygus sp.* (off-centre X bars) | *Cispeltinus maculosus* | *Conusphaera rothii* | *Conusphaera* cf. *rothii* (shorter than wide) | *Cretarhabdus angustiforatus* | *Cretarhabdus conicus* | *Cretarhabdus crenulatus* | *Cretarhabdus madingryensis* | *Cretarhabdus octoliesthrus* | *Cretarhabdus radiatus* (rare) | *Cretarhabdus schizobrachiatus* | *Cretarhabdus surirellus* | *Cretarhabdus trequetis* | *Cretarhabdus* indet. | *Crucibiscutum hayi* | *Crucibiscutum salebrosum* | *Crucibiscutum Tiphinatus* | *Crucicalyptra cuvillieri* | *Cyclagelosphaera argenensis* | *Cyclagelosphaera Tiangii* | *Cyclagelosphaera margerelii* | *Cyclagelosphaera papilla* (>6µ dia.) | *Cyclagelosphaera papilla* (<6µ dia.) | *Cyclagelosphaera Trotosiynaste* | *Diadorhombus rectus* | *Diloma galicienee* | *Diloma primitiva* | *Diloma? sp.1* | *Discorhabdus ignotus* | *Ethelinthus aristatus* | *Ethelintus windii* | *Ethelintus sp.1* | *Ethnorhabdus haroldwhitei* | *Gartnerlithus meddii* | *Hocus circumradiatus* | *Hocus elliptocus* | *Hocus indet.* | *Holmes chiasta* | *Holmes concus* | *Holmes staurolithina* | *Hemipodorhabdus gorkae* | *Hemipodorhabdus sp.* | *Lapidocassis glans* | *Lapidocassis manae* | *Lithraphidites bollii* | *Lithraphidites carniolensis* | *Lucilithus armilla* | *Manivitella pemmatoidea* | *Markalius sp.* (circular) | *Markalius? sp.* (elliptical) | *Micrantholithus hoschulzii* | *Micrantholithus obtusus* | *Micrantholithus speetonensis* | *Micrantholithus sp.1* (circular) | *?Watznaueria fenula* | *Nannoconus incmatus var.1* | *Nannoconus incmatus var.2* (small) | *Nannoconus abundans var.1* (narrow flange) | *Nannoconus abundans var.2* (wide flange) | *Nannoconus sp.* (short, bi-flanged) | *Nannoconus sp.* (tall, flangeless) | *Nannoconid cf. N.bucheli blokkes* | *Nannoconus bucheli* | *Nannoconus kamptneri* | *Nannoconus wintoni* | *Nannoconus globulus globulus* | *Nannoconus kamptneri* | *Nannoconus steinmanni* | *Nannoconid debris* (Abundant/Very Abundant) | *Neopatellalithus stubdingali* | *Neopatellalithus sp.1* | *Parcivilla fenestrata* | *Parhabdolithus indetus* | *Partaxocyclus plethotreta* | *Partaxocyclus tayloriea* | *Partaxocyclus* indet. | *Pickethaulus fulvia* | *Pickethaulus antiquus* | *?Rangilum parvidentatum* | *Rhagodiscus angustus* | *Rhagodiscus asper* | *Rhagodiscus infinitus* | *Rhagodiscus pseudorugosus* var.1 (angular) | *Rhagodiscus pseudorugosus* var.2 (rounded) | *Rhagodiscus reinhardtii* | *Rotelapillus laffittei* | *Rotelapillus windleyes* | *Staphilithus bisetrix* | *Stoverius hortices* | *Stoverius bowii* | *Stoverius* indet. | *Speetonia colligata* | *Tiarumitholus crux* | *Tiarumitholus michienarii* | *Tiarumitholus sp.1* (bicyclic rim) | small *Staurolithites* spp. | *Stephanolithion atmetos* | *Stradnerithus geometricus* | *Stradnerithus hexamerius* | *Stradnerithus silvaradius* | *Tegulithus septentrionalis* | *Tegumentum bergeri* var. *bergeri* | *Tegumentum bergeri* var. *minutus* | *Tegumentum bergeri* var. *quasiocellatus* | *Tegumentum cotitrmis* | *Tetrapodorhabdus decorus* | *Tranolithus gabalus* | *Tranolithus sp.* | *Tranopelorhabdus spematosa* | *Triquetrorhabdulus shetlandensis* large var. | *Triquetrorhabdulus shetlandensis* small var. | *Triquetrorhabdulus? sp.1* (square ended) | *Tubodiscus jurapelagicus* | *Tubodiscus parvus* | *Tubodiscus semesae* | *Watznaueria barnesae* | *Watznaueria britannica* | *Watznaueria communis* | *Watznaueria fossacincta* | *Watznaueria manivitae* | *Watznaueria ovata* | *Watznaueria? fossacincta* | *Watznaueria? tipo1* | small indet. *Watznauerla* | *Zeugrhabdotus diplogrammus* | *Zeugrhabdotus xenhilmii* | *Zeugrhabdotus "elegans"* | *Zeugrhabdotus embergeri* | *Zeugrhabdotus erectus* | *Zeugrhabdotus* sp. cf. *Z.erectus* | *Zeugrhabdotus noelae* | *Zeugrhabdotus scutula* | *Zeugrhabdotus trivectis* | *Zeugrhabdotus* sp. (cf. *Z.noelae*, but larger) | *Spicula* sp.1 (tetractine) | *Spicula* sp.2 (pair-shaped, 3 nodes) | *Nannofossil* sp. (bundled spicular aggregate) | *Micrascidites?* sp. (fusiform spicules) | DEPTH (metres) | AGE |
|---|---|---

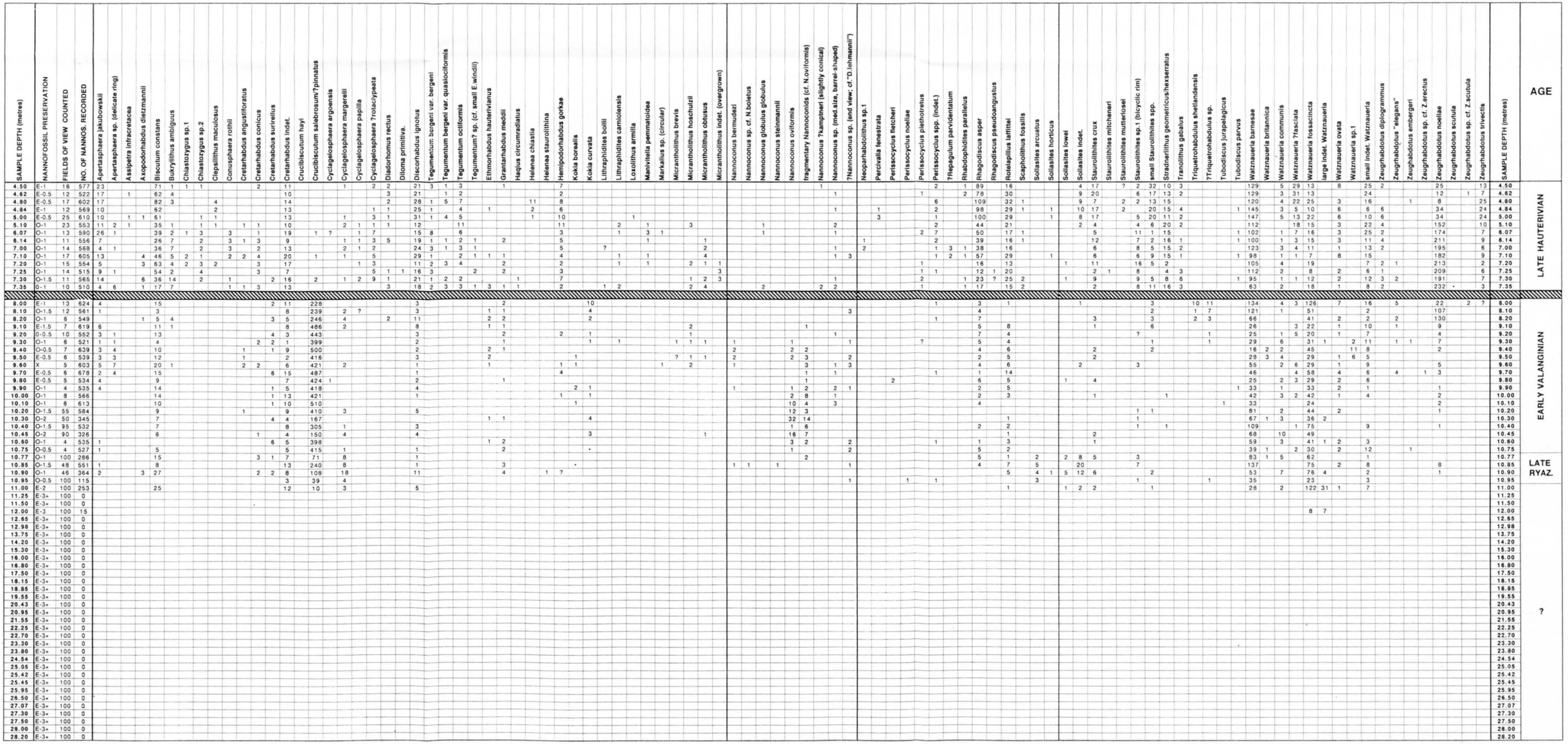


Chart 4 - Core 7B (offshore mid-Norway)

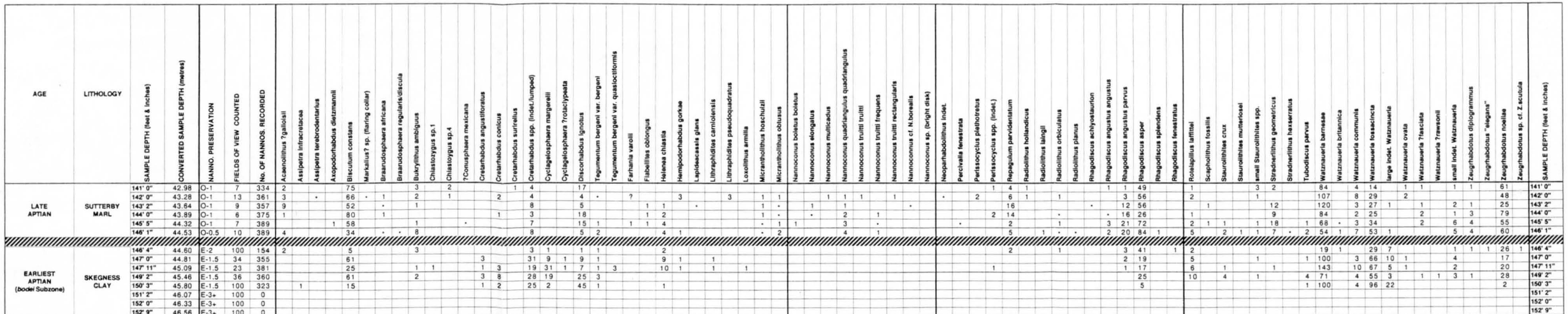
Stratigraphical distribution of calcareous nannofossils in Core 7B. The hatched area represents a stratigraphical break.

| SAMPLE DEPTH (metres) | NANNOFOSSIL PRESERVATION | NO. OF NANNOS RECORDED | FIELDS OF VEIW COUNTED | Apertasphaera jakubowskii | Axopodorhabdus dietzmannii | Biscutum constans | Bukrylithus ambiguus | Chiastozygus sp.2 (recurved X-bars) | Chiastozygus sp. (small; misaligned X) | Conusphaera rothii | Cqnusphaera aff. rothii (short cone) | Cretarhabdus angustiforatus | Cretarhabdus conicus | Cretarhabdus spp. (indet.) | Crucibiscutum hayi | Crucibiscutum salebrosum/?plnnatus | Cyclagelosphaera argoensis | Cyclagelosphaera margerelii | Cyclagelosphaera papilla (<8µ dia) | Discorhabdus ignotus | Eiffellithus striatus | Hemipodorhabdus gorkae | Kokia borealis | Kokia curvata | Loxolithus armilla | Manivitella pemmatoidea | Markalius sp. (circular) | Micrantholithus hoschulzii | Micrantholithus obtusus | Neoparhabdolithus sp.1 | Perissocyclus plethotretus | indet. Podorhabdid rims | Radiolithus antiquus | Rhagodiscus asper | Rhagodiscus pseudoangustus | Rotelapillius laffittei | Sollasites arcuatus | Sollasites horticus | Sollasites lowei | Sollasites indet. | Staurolithites crux | Staurolithites mitcheneri | ?Staurolithites glabra | small Staurolithites spp. | Stradnerlithus geometricus | Tegulalithus septentrionalis | Tegumentum bergeni var. bergeni | **Tegumentum bergeni var. minutus (rima)** | Tegumentum bergeni var. quasioctiformis | Tranolithus gabalus | Triquetrohabdulus shetlandensis | ?Triquetrohabdulus sp. (no clear "keel") | Watznaueria barnesae | Watznaueria britannica | Watznaueria communis | Watznaueria fossacincta | large indet. Watznaueria | Watznaueria ovata | Watznaueria ?fasciata | small indet. Watznaueria | Zeugrhabdotus diplogrammus | Zeugrhabdotus embergeri | Zeugrhabdotus sp. cf. Z.erectus | Zeugrhabdotus noeliae | Zeugrhabdotus trivectis | SAMPLE DEPTH (metres) | AGE |
|---|---|---

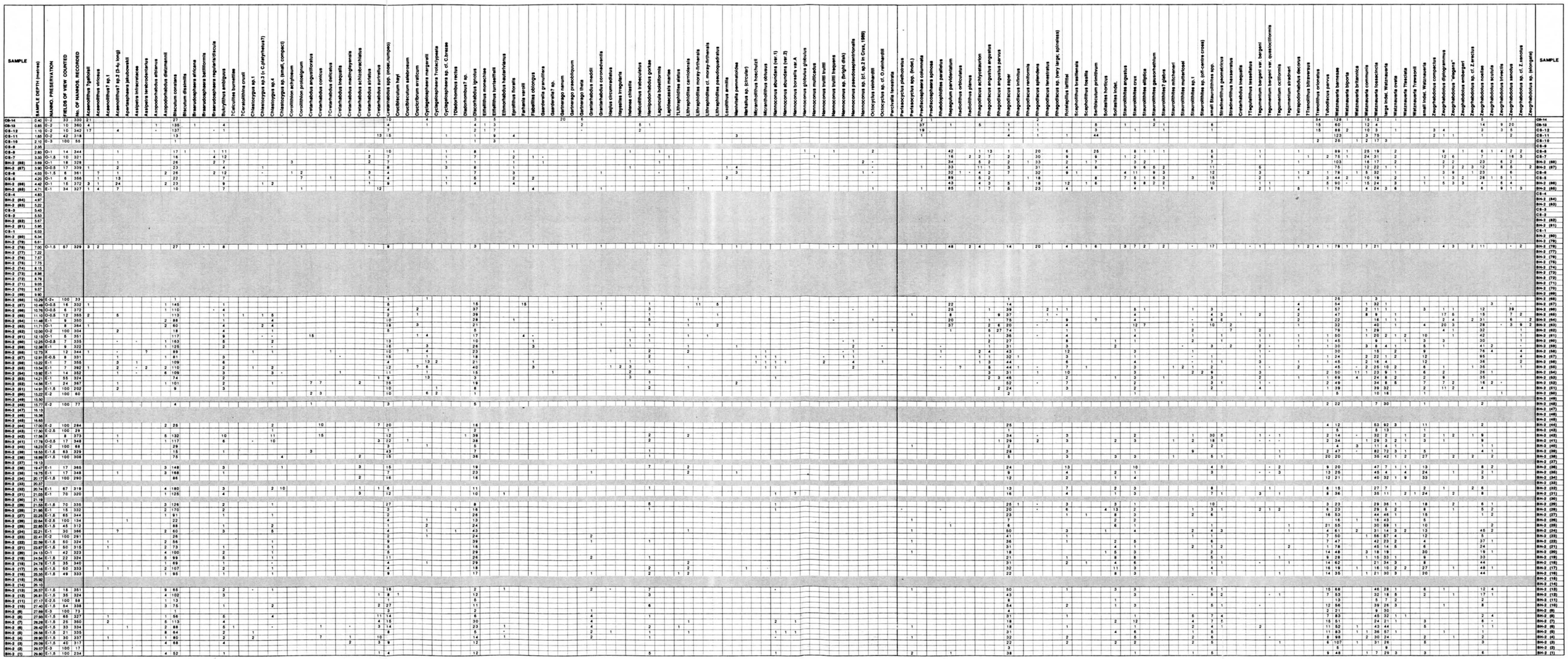
Chart 6 - Core 7430/10-U-1 (Barents Sea)

Stratigraphical distribution of calcareous nannofossils in Core 7430/10-U-1. Bold horizontal lines represent possible stratigraphical breaks.

| SAMPLE DEPTH (metres) | NANNOFOSSIL PRESERVATION | NO. OF NANNOS RECORDED | FIELDS OF VEIW COUNTED | Apertasphaera jakubowskii | Assipetra infracretacea | Axopodorhabdus dietzmannii | Biscutum constans | Calculites burnettiae | Chiastozygus sp.1 | Chiastozygus sp.2 (recurved X-bars) | Chiastozygus sp. (small; misaligned X) | Conusphaera rothii | Cretarhabdus angustiforatus | Cretarhabdus conicus | Cretarhabdus schizobrachiatus | Cretarhabdus surirellus | Cretarhabdus spp. (indet.) | Crucibiscutum salebrosum | Cyclagelosphaera argoensis | Cyclagelosphaera ?brezae | Cyclagelosphaera margerelii | Cyclagelosphaera papilla (<8μ dia.) | Cyclagelosphaera papilla (8μ+) | Discorhabdus ignotus | Eiffellithus striatus | ?Eiffellithus sp.1 | Hemipodorhabdus gorkae | Kokia curvata | Loxolithus armilla | Maniviteila pemmatoidea | Markalius sp. (circular) | Micrantholithus spp. (overgrown) | Nannoconus abundans | Nannoconus pseudoseptentrionalis | Neoparhabdolithus sp.1 | Perissocyclus plethotretus | Rhagodiscus asper | Rotelapillus laffittei | Solllasites arcuatus | Solllasites horticus | Solllasites indet. | Stauroilthites crux | Stauroilthites mitcheneri | small Stauroilthites spp. | Tegumentum bergeni | Tegumentum bergeni var. quasioctiformis | Tranolithus gabalus | Triquetrohabdulus shetlandensis | ?Triqetrohabdulus sp. | Tubodiscus parvus | Watznaueria barnesae | Watznaueria britannica | Watznaueria communis | Watznaueria fossacincta | large indet. Watznaueria | Watznaueria ovata | Watznaueria ?fasciata | small indet. Watznaueria | Zeugrhabdotus noeliae | Zeugrhabdotus trivectis | Zeugrhabdotus sp. cf. Z.embergeri | Zeugrhabdotus sp. cf. Z.erectus | Zeugrhabdotus sp. cf. Z.scutula | Zeugrhabdotus sp. cf. Z.xenotus | SAMPLE DEPTH (metres) | AGE |
|---|---|---



| AGE | LITHOLOGY | SAMPLE DEPTH (feet & inches) | CONVERTED SAMPLE DEPTH (metres) | NANNO. PRESERVATION | FIELDS OF VIEW COUNTED | No. OF NANNOS. RECORDED | Acaenolithus ?galloisii | Assipetra infracretacea | Assipetra terebrodentarius | Axopodorhabdus dietzmannii | Biscutum constans | Markalius? sp. (flaring collar) | Braarudosphaera africana | Braarudosphaera regularis/discula | Bukrylithus ambiguus | Chiastozygus sp.1 | Chiastozygus sp.4 | ?Conusphaera mexicana | Cretarhabdus angustiforatus | Cretarhabdus conicus | Cretarhabdus surirellus | Cretarhabdus spp. (indet./lumped) | Cyclagelosphaera margerelii | Cyclagelosphaera ?rotaclypeata | Discorhabdus ignotus | Tegumentum bergenii var. bergenii | Tegumentum bergenii var. quasioctiformis | Farhania varolii | Flabellites oblongus | Helenea chiastia | Hemipodorhabdus gorkae | Lapideacassis glans | Lithraphidites carniolensis | Lithraphidites pseudoquadratus | Loxolithus armilla | Micrantholithus hoschulzii | Micrantholithus obtusus | Nannoconus boletus boletus | Nannoconus elongatus | Nannoconus multicadus | Nannoconus quadrianguius quadrianguius | Nannoconus truitti truitti | Nannoconus truitti frequens | Nannoconus truitti rectangularis | Nannoconus cf. N.borealis | Nannoconus sp. (bright disk) | Neoparhabdolithus indet. | Percivalia fenestrata | Parissocyclus plethotratus | Parissocyclus spp. (indet.) | Repagulum parvidentatum | Radiolithus hollandicus | Radiolithus laingii | Radiolithus orbiculatus | Radiolithus planus | Rhagodiscus achlyostaurion | Rhagodiscus angustus angustus | Rhagodiscus angustus parvus | Rhagodiscus asper | Rhagodiscus splendens | Rhagodiscus fenestratus | Rotelapillus laffittei | Scapholithus fossilis | Staurolithites crux | Staurolithites mutteriosei | small Staurolithites spp. | Stradnerlithus geometricus | Stradnerlithus hesserratus | Tubodiscus parvus | Watznaueria barnesae | Watznaueria britannica | Watznaueria communis | Watznaueria fossacincta | large indet. Watznaueria | Watznaueria ovata | Watznaueria ?fasciata | Watznaueria ?rawsonii | small indet. Watznaueria | Zeughrabdotus diplogrammus | Zeughrabdotus "elegans" | Zeughrabdotus noeliae | Zeughrabdotus sp. cf. Z.scutula | SAMPLE DEPTH (feet & inches) |
|---|---|---


SAMPLE
SAMPLE DEPTH (metres)
NANNO. PRESERVATION
FIELDS OF VIEW COUNTED
No. OF NANNOS. RECORDED
Acaenolithus ligaforsii
Acaenolithus sinosus
Acaenolithus? sp.3 (3-4µ, long)
Apertapetrahere jakubowskii
Assipetra infracretacea
Assipetra terebrodentaria
Aspidodonhabdus ehrhenia
Aspidodonhabdus dietzmanii
Blackites constans
Blackites dissimilis
Braarudosphaera africana
Braarudosphaera bigelowii
Braarudosphaera regularis/discula
Butrylithus ambiguus
Calculites burnettiae
Ceratolithina cruciii
Chiasmolithus sp.1
Chiasmolithus sp.3 (c.f.oamaruensis?)
Chiasmolithus sp.4
Chiasmolithus sp. (small, compact)
Cocolithion actylosum
Cocolithion protostegium
Cretarhabdus angustiforatus
Cretarhabdus conicus
Cretarhabdus crenulatus
Cretarhabdus delicatus
Cretarhabdus hoequistii
Cretarhabdus madingayensis
Cretarhabdus schizobrachiatus
Cretarhabdus striatus
Cretarhabdus surirellus
Cruciplacolithus spp. (indet./complex)
Cruciplacolithus tenuis
Crucibiscutum hayi
Crucibiscutum salebrosum
Cruciellipsis cuvillieri
Cyclagelosphaera margerelii
Cyclagelosphaera Trochecypsella
Cyclagelosphaera sp. cf. C.braae
Diadomhombus rectus
Diadomhombus? sp.
Discorhabdus ignotus
Discorhabdus rotundus
Ellipsagelosphaera britannica
Ellipsagelosphaera communis
Ellipsagelosphaera deflandrei
Ellipsagelosphaera floralis
Eprolithus floralis
Fasciculithus tympaniformis
Fasciculithus? sp.
Fasciculithus? sp. (cf. F.tympaniformis)
Fasciculithus? sp. (cf. F.tympaniformis)
Fasciculithus? sp. (cf. F.tympaniformis)